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MICHIGAN ACADEMY OF SCIENCE ARTS AND LETTERS

VOLUME XIII

CONTAINING PAPERS SUBMITTED AT THE ANNUAL MEETING IN 1930

(This volume contains papers in Botany and Zoölogy only Volume XIV will contain papers in Anthropology Economics and Sociology History and Political Science, Geography, Geology and Mineralogy Language and Literature, Mathematics Meteorology and Sanitary and Medical Science)

PAPERS
OF THE
MICHIGAN ACADEMY OF SCIENCE ARTS AND LETTERS

EDITORS
EUGENE S. McCARTNEY
UNIVERSITY OF MICHIGAN
PETER OKKELBERG
UNIVERSITY OF MICHIGAN

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INHERITANCE OF DWARF IN CAPSICUM *

ERNEST F DALE

WHEN dwarf plants first appeared in a culture of the pepper variety Coral Gem, it was assumed that they were caused by disease The dwarfs were abnormal in appearance, averaged about six inches in height, had crinkled leaves and bore few fruits Normal Coral Gem plants were about twelve inches in height, had smooth leaves and produced abundant fruits The data presented in this paper were secured incidentally during the course of a study of inheritance of fruit-length in crosses between the varieties Coral Gem and Anaheim [1] Not until the second generation by self-pollination after back-crossing (Table III) was grown, was it realized that dwarf was an inherited characteristic The data on the occurrence of dwarf in the variety Coral Gem are thus somewhat scanty

Inasmuch as the data chiefly relied upon to demonstrate the inheritance of dwarf (Table III) involve the segregation of dwarf plants from a mixed Coral Gem–Anaheim parentage, data on the occurrence of dwarf in both the Anaheim and Coral Gem varieties are given in Table I The data in Table I suggest that Coral Gem was heterozygous for dwarf and that dwarf behaved as a simple recessive The single dwarf Anaheim plant in family 25 1 appeared to be diseased and did not produce fruit Coral Gem dwarfs, as before stated, normally set fruits The absence of dwarfs from the other Anaheim families indicates that the dwarf in family 25 1 was due to disease or to some unfavorable growth condition Since this plant produced no fruit, it was impossible to determine whether the condition was inherited

Table II shows the behavior of dwarf in the F_1 and F_2 generations when crossed with Anaheim The F_1 plants were all normal

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* Paper from the Department of Botany, University of Michigan, No 338

[1] Dale E E *Pap Mich Acad Sci, Arts and Letters,* 9 89-110 1928

TABLE I

DWARF AND NORMAL PLANTS IN THE PEPPER VARIETIES ANAHEIM AND CORAL GEM

Family Number	Parentage	Normal	Dwarf
23 1	Anaheim self pollinated	48	0
25 1	do	55	1
25 75	do	58	0
27 16	do	98	0
23 4	Coral Gem self pollinated	16	4
25 96	do	34	11

TABLE II

F_1 AND F_2 GENERATIONS OF CROSSES BETWEEN CORAL (HETEROZYGOUS FOR DWARF) AND ANAHEIM

Family Number	Parentage	Normal	Dwarf
23 2	F_1 Anaheim ♀ × Coral Gem ♂	48	0
23 3	F_1 Coral Gem ♀ × Anaheim ♂	56	0
25 2	F_2 (Anaheim ♀ × Coral Gem ♂)	183	53
25 3	F_2 (Coral Gem ♀ × Anaheim ♂)	102	1

in appearance, an indication that the character was recessive The two F_2 families, 25 2 and 25 3, came from reciprocal F_1 crosses One of these showed segregation for dwarf, the other did not If, as the data of Table I indicate, the original Coral Gem parent was heterozygous for dwarf, the F_1's would be of two types, hetero-

TABLE III

SEGREGATION FOR DWARF IN THE SECOND GENERATION BY SELF POLLINATION AFTER THE BACK CROSS CORAL GEM × (CORAL GEM × ANAHEIM) AND THE RECIPROCAL BACK-CROSS

Family number	Parentage	Normal	Dwarf
A 25 5	Coral Gem ♀ × (Coral Gem × Anaheim ♂)	58	17
A 25 10		101	34
A 25 11		92	19
A 25 13		86	35
A 25 17		52	24
A 25 18		84	25
A 25 19		51	15
A 25 21		92	29
A 25 23		70	26
A 25 24		44	19
A 25 38		69	8
A 25 40		102	33
A 25 41		56	17
A 25 43		120	64
A 25 46		80	18
A 25 49		67	38
A 25 51		123	33
A 25 52		64	15
A 25 53		55	19
A 25 65		75	27
A 25 66		43	27
A 25 68		52	11
A 25 69		99	34
A 25 100		109	44
A 25 101		75	29
	Total	1919	660
B 25 26	(Coral Gem × Anaheim ♀) × Coral Gem ♂	46	18
B 25 32		93	29
B 25 56		54	21
B 25 62		55	26
B 25 63		24	5
B 25 70		98	20
B 25 74		88	17
	Total	458	136
	TOTAL (Series A and B)	2377	796

zygous dwarf and homozygous not-dwarf Thus it would be expected that half of the F_2 families would show segregation for dwarf and half would produce only normal plants Twenty-two per cent of the offspring in family 25 2 were dwarfs, a result which conforms to the monohybrid expectation The dwarf plant in family 25 3, like the dwarf individual in family 25 1, Table I, is assumed to have resulted from some growth disturbance

In Table III, families A 25 5 to A 25 101 were the progeny of self-pollinated plants of the back-cross Coral Gem × (Coral Gem × Anaheim), and families B 25 26 to B 25 74, came from self-pollinated plants of the back-cross (Coral Gem × Anaheim) × Coral Gem The table lists only those families which showed segregation for dwarf Families A 25 5 to A 25 101 gave a progeny of 1919 normal and 660 dwarf plants Families B 25 26 to B 25 74 gave 458 normals and 136 dwarfs The total for both groups was 2377 normals and 796 dwarfs, or 25 09 per cent of dwarfs Such a very close approximation to a monohybrid expectation leaves no doubt that dwarf behaved as a simple recessive character

Examination of Table III shows some marked departures from the expected ratios, 10 per cent of dwarfs in family A 25 38 and 39 per cent in family A 25 66 Thus family A 25 38 was 15 per cent too low and family A 25 66 was 14 per cent too high The departures offset each other, which indicates that they may have been due to random variations

It was to be expected that self-pollination of the heterozygous Coral Gem parent would produce a pure not-dwarf strain Such a pure strain of normal plants was obtained from a self-pollinated plant of family 25 96, Table I

SUMMARY

A dwarf type of pepper showed recessive monohybrid inheritance

UNION COLLEGE
SCHENECTADY, NEW YORK

MATERNAL INHERITANCE IN A CHLOROPHYLL VARIEGATION IN CAPSICUM *

ERNEST L. DALE

A SINGLE variegated pepper plant appeared in the progeny of a back-cross, Coral Gem × F_1 (Coral Gem × Anaheim) When the plant was first observed one cotyledon and two of the leaves were quite pale and apparently without chlorophyll Two leaves were green on one side of the midrib and pale on the other Two other leaves showed irregular yellowish and green areas, the margins of which areas were sharply defined The second cotyledon and the remaining leaves were green There were seventy nine back-cross progeny The Coral Gem and Anaheim parents were under observation for seven generations and during this time neither produced any variegated plants

Plate I, Figure 1, shows the characteristic appearance of a variegated plant In addition to the variegated branch at the lower left there were smaller variegated branches in the middle portion of the plant, but only a small proportion of the whole plant was variegated The effect of the variegation upon the leaves is shown in Plate I, Figure 2 The pale areas varied in color from nearly white (without chlorophyll) to yellowish-green The yellowish-green color appeared to be produced where green tissue was overlain by tissue without chlorophyll or the reverse The non-green parts will hereafter be referred to as white Variegation was quite as strikingly shown in the fruits as in the leaves, although this is not brought out in the plate The variegated fruits showed clearly defined sectors of pale and green tissue In habit and in the size and shape of the fruits, the variegated plant, except that it was somewhat larger, was much like the original Coral Gem parent

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* Paper from the Department of Botany University of Michigan No 337

In the study of the inheritance of the variegation, self-pollinations and crosses were made by using flowers on both the variegated and normal green branches of the variegated plant The results are shown in Table I Self and cross-pollinated flowers on green branches gave only green offspring, families 27 1, 27 5, 27 6, 28 1, 28 2 and 28 9 Self pollinated flowers on white branches produced pale offspring, families 27 3 and 27 4, and these died in the seedling stage The pale seedlings at first possessed some chlorophyll, being greenish yellow They gradually lost their chlorophyll, however The cotyledons of the pale plants were approximately normal in size The plumules failed to develop Crosses with flowers on white or variegated branches, families 27 8, 28 6 and 29 1, showed maternal inheritance, inasmuch as pale or variegated (one plant) offspring appeared only when white or variegated was used as the pistillate parent It is noticeable that out of five families which produced pale offspring, only one, 27 8, produced a variegated plant The twenty progeny in family 27 8 came from seed of a single fruit, the product of the cross White ♀ × Coral Gem ♂ The variegated individual could be accounted for by assuming that the supposed white branch used in the parent cross was in reality variegated, but had only a very small amount of green tissue The fact that only one of the twenty seedlings in the family possessed green tissue throws some doubt on such an explanation The variegation could also be explained as the result of a new mutation from white to green

In family 29 1 crosses were made by using flowers on variegated instead of white branches As might have been expected, this cross produced a mixed progeny of pale and green plants Out of sixty-eight seedlings twenty were pale and soon died The rest were normal green plants

Correns (1902, 1909) described a chlorophyll variegation in Mirabilis which showed maternal inheritance He explained the non-Mendelian inheritance of the variegation as due to its transmission through the cytoplasm Baur (1909) suggested that the inheritance of the variegation in *Pelargonium zonale* was through the plastids The *zonale* character was transmitted through both the male and female gametes The theory of the transmission

TABLE I

PROGENY FROM SELF AND CROSS-POLLINATIONS ON GREEN WHITE AND VARIEGATED BRANCHES OF VARIEGATED PEPPER PLANT

Family number	Parentage	Green	Pale	Variegated
27 1	Green branch self pollinated	103	0	0
27 3	White self pollinated	0	18 (died)	0
27 4	White self pollinated	0	30 (died)	0
27 5	Coral Gem ♀ × White ♂	44	0	0
27 6	Coral Gem ♀ × White ♂	102	0	0
27 8	White ♀ × Coral Gem ♂	0	19 (died)	1
28 1	Coral Gem ♀ × White ♂	78	0	0
28 2	Coral Gem ♀ × White ♂	53	0	0
28 6	White ♀ × Anaheim ♂	0	2 (died)	0
28 9	F₁ (Coral Gem ♀ × White ♂)	115	0	0
29 1	Variegated ♀ × Coral Gem	68	29 (died)	0

of variegation through the plastids has been widely adopted in explanation of maternal inheritance of chlorophyll variegations Demerec (1927) inclines to the cytoplasmic explanation of the transmission of such characters, but states also that an explanation based upon mutable genes is not excluded

Both the appearance of the plant, as shown in Plate I, and the genetic behavior of the character indicate that the variegation here reported was of the sectorial-chimera type The data conform to the plastid theory of the inheritance of chlorophyll variegations, but they are not of such a nature as to give evidence concerning the mutable-gene hypothesis

SUMMARY

A chlorophyll variegation appeared in a back-cross between two varieties of peppers The variegation showed maternal inheritance

UNION COLLEGE
SCHENECTADY, NEW YORK

LITERATURE CITED

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—— 1909 Vererbungsversuche mit blass (gelb) grunen und buntblättrigen Sippen bei *Mirabilis Jalapa, Urtica pilulifera* und *Lunaria annua* Zeitschr Indukt Abstamm Vererb., 1 291–329

DEMEREC, M 1927 A Second Case of Maternal Inheritance of Chlorophyll in Maize Bot Gaz , 84 139–155

PLATE I

Fig 1 Capsicum variegated plant of intervarietal cross

Fig 2 Leaves of plant shown in Figure 1

VEGETATION OF THE PORCUPINE MOUNTAINS, NORTHERN MICHIGAN

PART I ECOLOGY

HENRY TOWNSEND DARLINGTON

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INTRODUCTION

IN HIS classic article on the climax forest of Isle Royale, Lake Superior, Cooper (6) refers to the transitional zone between the two great phytogeographic regions, the northeastern conifer and the eastern deciduous forest Certain features of both regions, he says, are found in the southwestern portion of the island, but he did not carry out his first intention of tracing the relations between them On the mainland of Michigan to the south, the maple forest is well developed, especially at certain inland points Areas near the coast, however, may show many transitional features such as occur in the Porcupine Mountains, which are about 125 km south southwest of Isle Royale These so-called mountains, which are really prominent hills or hilly ridges, represent the highest points of land reached in the Upper Peninsula As Leverett (22) points out, they are "the most conspicuous features in this entire area, for they rise on their north slope very abruptly from the shore of Lake Superior to a height of 1400 feet above the lake"

The Porcupine Mountains consist roughly of three ranges of hills, paralleling the coast (Pl II, Fig 1), that nearest the shore being the most rugged Back of these lies a table-land stretching south to the Gogebic Range

It was not found possible to examine all of this territory, nor does it seem essential to an understanding of the vegetational development of the region Practically all the detail studies were made in connection with the first range and the valley of Carp River behind it It must be admitted that this near-shore region received most attention because of its greater accessibility, yet aside from this it seemed of major importance for the following reasons (1) the pioneer conditions found on the first range, where the summit still remains unclaimed by vegetational development, (2) the nearness of Lake Superior, permitting the observation of various stages of succession along the shore, (3) the proximity of a comparatively high altitude (for the region) to the wind-swept surface of Lake Superior, giving a definiteness to the larger problems of vegetation, (4) a forest covering which gives it unusual value for a study of the relation between two climax formations, (5) opportunity for observing practically primeval forest conditions

Field work was carried out in the summer of 1922 Headquarters were first established at a point on Union Bay (Section 16, T 51 N, R 42 W) This was found to be the most convenient location for the examination of the shore-line and the hemlock forest of the north slope Later, headquarters were located on the site of an old mining property near Carp Lake All the work in connection with Carp River Valley and the summit of the range was done from this point

The nomenclature used in connection with the pteridophytes and spermatophytes is that of Gray's *Manual*, seventh edition

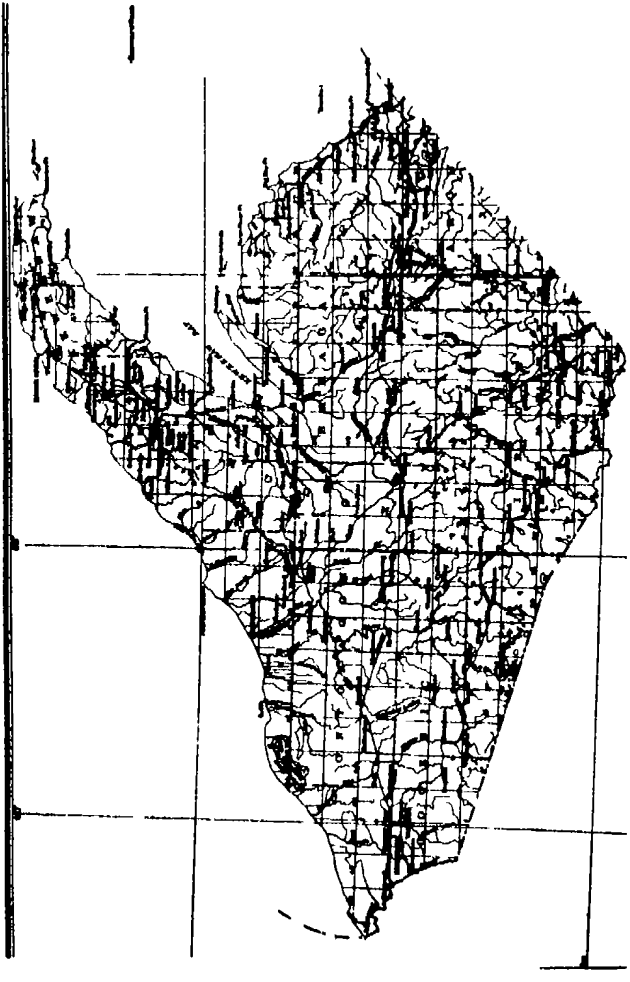
EARLIER INVESTIGATIONS IN THE PORCUPINE MOUNTAINS

The early interest attaching to an exploration of the mountains was based on the prospect of finding copper Indications of this interest are shown in the abandoned shafts and workings in various parts of the region In 1848 the mountains were visited by W D Whitney (13) acting as botanist on a government expedition in charge of J W Foster The following year several places on the south shore of Lake Superior were visited — as far west, Whitney says, as the Ontonagon Valley and Carp River, both in the vicinity of the Porcupines In the second report on the region (14), which was published in 1851, Whitney gives a list of plants seen in the Upper Peninsula, including some from Isle Royale This list, being very general, gives no clue as to what species were observed in the Porcupine Mountains In Jackson's *Lake Superior* (3), published in 1849, Bela Hubbard, a geologist, in discussing the origin and character of the soil in the Porcupines, points out that the sugar maple predominates throughout the elevated portions, while hemlock is the prevailing tree upon the lower lands

During the next fifty years apparently little was done in the way of botanical investigation in this region In the summer of 1903, F E Wright (30), assistant state geologist, continued the work, earlier begun under the direction of Dr L L Hubbard, of preparing data for an accurate geological report and map of the mountains During a part of this time he was accompanied by Dr A G Ruthven of the University of Michigan, who became interested in the biological aspects of the country In 1904 and 1905 the University Museum sent parties to northern Michigan to make biological studies in the Porcupine Mountains and on Isle Royale One party, led by Dr Ruthven, spent one month in the Porcupines and the remainder of the season on Isle Royale The report of this expedition (1) came out in 1905 It covers both regions, listing ninety-one species of plants and noting the ecological distribution of the more important species

LOCATION AND PHYSIOGRAPHY

The Porcupine Mountains are in Ontonagon County in the Northern Peninsula of Michigan, in lat 47 N , long 90 W (see Map 1) Their unique position, close to the south shore of Lake Superior, has already been pointed out They reach a maximum altitude of 618 m above sea-level, or 435 m above the level of the lake The top of the first range or ridge comes within 2 km of the shore Its north slope is rather gentle, but becomes increasingly steep as one approaches the summit, finally reaching a height of 275 m above the lake in Section 14, T 51 N , R 43 W There is then a sudden descent of about 120 m to the valley of Carp River, half of this descent being, in places, vertical rock face At the base of the cliff there is a talus slope extending in places several hundred meters down the side of the valley This great cliff extends for a distance of about 10 km across T 51 N , R 43 W It is interesting to note Foster's impressions on first seeing this great outcropping of rock in 1848 He says "Suddenly the traveler finds himself on the brink of a precipice five hundred feet deep, at the base of which lies a small lake, so sheltered and hemmed in by the surrounding mountains that the wind rarely ripples the surface Gloomy evergreens skirt its shores, whose long and pendant branches are so faithfully reflected on the surface that the eye can with difficulty determine where the water ends and the shore begins From this lake flows the Carp River, and



MAP 1 General position of the Porcupine Mountains in Ontonagon County, Upper Peninsula of Michigan

the beholder occasionally catches a glimpse of its waters as they wind through the narrow valley towards the great reservoir"

Geologically, the mountains form a crescent-shaped offshoot or spur from the main range to the south (Fig 1) This extends from Keweenaw Point southwest to Wisconsin, including the well-known iron and copper ranges of the Keweenaw Series The ranges

Fig 1 Geological map of a portion of the Porcupine Mountains showing their relation to the Keweenaw Series to the south (after Irving)

of the Porcupines consist largely of eruptive rocks with interbedded sandstones and conglomerates, the strata tilted from 30 to 40 degrees They represent part of a pre-Cambrian upheaval, probably during early Proterozoic time The present system of hills forms a comparatively small portion (Fig 2) of the original land mass, the rest having been removed by erosion during a very long period of time

At the beginning of the glacial period the general topography

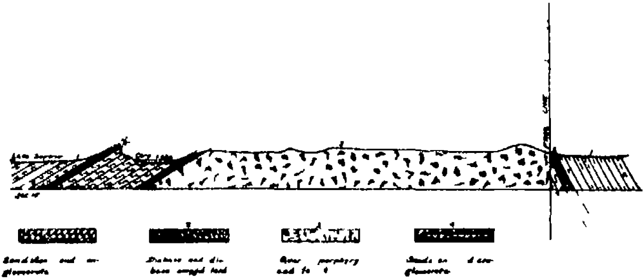


Fig 2 Geological sections illustrating the structure of the Porcupine Mountains (after Irving)

was probably much the same as at present The mountains were laid bare at a relatively early date, making a cusp in the ice front, presumably between the Warren and Algonquin stages According to Lane (21), the water was ponded on the north side of the mountains to a depth of 171 m above the present surface of Lake Superior and on the south side at least 49 m higher than this, the drainage being toward the Mississippi Old beach lines on the north slopes show successive stages in the height of the lake, where the lake level was more or less stationary

From what has been said, it is evident that the higher level lies back of the first range, though the latter is much the more rugged The rough topography is, in general, conditioned by the geologic structure of the region The main drainage lines are occupied by the Carp and Little Carp rivers, which flow approximately southwest These parallel the general direction of the ridges and finally turn northwest, emptying into Lake Superior A portion of the drainage is also east and southeast into the valley of Iron River

CLIMATE OF THE REGION

The following data were obtained through the courtesy of the U S Weather Bureau at East Lansing (see also report by Seeley, 26) It is believed that Tables I and II taken together give a fair index of the climatic conditions Bergland, representing inland conditions, is about 27 km south-southeast of Carp Lake, it has an elevation of 215 m above the surface of Lake Superior Ontonagon is situated at the mouth of the Ontonagon River, 32 km east of Bergland The tables show that the mean temperature for the year is very nearly the same for both places

TABLE I

MEAN TEMPERATURE AT BERGLAND FOR 11 YEARS

	Jan	Feb	March	April	May	June	
C	− 12 9	− 11 4	− 4 1	4 1	10 5	16 3	
	July	Aug	Sept	Oct	Nov	Dec	Yr
C	18 6	16 9	12 7	6 8	− 0 2	− 7 7	4 1

TABLE II

MEAN TEMPERATURE AT ONTONAGON FOR 7 YEARS

	Jan	Feb	March	April	May	June	
C	− 9 3	− 10 8	− 3 5	3 8	9 2	13 5	
	July	Aug	Sept	Oct	Nov	Dec	Yr
C	17 8	17 4	14 0	9 4	0 7	− 5 8	4 2

The differences in the average monthly temperatures of the two places indicate the probable moderating influence of the large body of water The average maximum temperature for 5 years at Ontonagon was 34 6° C and the average minimum − 29 7° C The mean monthly temperature at Bergland for 11 years was above 0° C for 7 months of the year, beginning with April, and the mean monthly minimum above this for 6 months, beginning with May Tables prepared by the U S Weather Bureau show that the average date of the last killing frost in spring is June 9, and that of the first killing frost in the fall is September 16, giving 89 days as the average length of the growing season In this region the isotherms parallel the shore-line, and the average temperature of points along the coast is several degrees warmer than inland points a few miles farther back During the hot summer months, however, the isotherms move back from the shore, so that the discrepancy between shore and inland conditions is not so great

TABLE III

AVERAGE MONTHLY PRECIPITATION AT BERGLAND FOR 11 YEARS

	Jan	Feb	March	April	May	June	
Cm	4.05	3.25	4.27	4.70	7.85	8.87	
	July	Aug	Sept	Oct	Nov	Dec	Yr
Cm	9.05	8.82	8.72	7.30	5.20	5.45	77.55

TABLE IV

AVERAGE MONTHLY PRECIPITATION AT ONTONAGON FOR 6 YEARS

	Jan	Feb	March	April	May	June	
Cm	5.95	4.65	3.89	2.61	5.72	5.25	
	July	Aug	Sept	Oct	Nov	Dec	Yr
Cm	11.57	8.42	9.27	4.37	5.85	7.02	74.57

These data, though not extending over as great a period of time as might be desirable, would seem to indicate that the average yearly rainfall for the region is about 76 cm. The figures show that the average precipitation along the coast during the months from November to February is 30 per cent greater than the precipitation at Bergland 26 km. back from the coast. This may help to explain certain striking differences between the vegetation near the shore and that farther inland. Slightly more than one half of the average rainfall occurs during the five months of the growing season (from May to September), apparently coming earlier in the season at inland points. The greatest average precipitation was in July.

The average number of cloudy days per month for five years at Ontonagon was fourteen, and partly cloudy five, leaving an average of one hundred thirty-seven clear days for the year. The prevailing direction of the wind at the same station is from the northwest, often veering around from the west.

The extent and ruggedness of the Porcupines allow for much local variation. These climatic data are not meant to be more than general. Their character accords with the general mesic character of the vegetation in its larger aspects.

THE CLIMAXES

There are two climaxes covering the ranges of the Porcupine Mountains On the north slope of the first range occurs a typical hemlock forest This gradually merges into a maple forest near the top of the slope From this point maple forms the climax on the ranges to the south, though scattered patches of hemlock occur on the lower slopes Any interpretation of the vegetation of the region must take into account the relation between these two climaxes, their relative position with respect to the larger physiographic features and the successions leading up to them In this paper the hemlock climax will be considered first

A THE HEMLOCK CLIMAX

This is apparently the most mesic formation of the region Its most typical development is on the lower half of the north slope of the first range It is composed largely of three tree species *Tsuga canadensis* (L) Carr (hemlock), *Acer saccharum* Marsh (sugar maple) and *Betula lutea* Michx f (yellow birch) At the lower levels near the lake shore the forest is almost entirely hemlock, while near the top of the ridge it merges into the less mesic maple forest

Intensive studies were made at various points in the forest with a view to determining the relations between the three principal species The life habits of each, from the seedling stage up, were studied as closely as time permitted Interrelations of the species were also studied by means of quadrats and windfall areas

I Aspect of the Forest

At first sight the forest appears to be almost a pure stand of hemlock The boles are conspicuous below, but the upper portions of the trees, which are 25–30 m or more tall, form a dense mass of interlaced foliage, with a ragged sky-line Here and there are occasional trees of yellow birch, with more open tops, also a few tall spindling maples, devoid of foliage, except near the summit, which often indicate by the presence of dead twigs the competition to which they are subjected

In Section 16, T 51 N , R 42 W , the hemlock had been removed from certain "forties," making it possible to obtain a view of the general composition of the forest from the outside This is shown in Plate II, Figure 2 The three species mentioned are practically the only ones in evidence from an exterior view of a section made in this part of the forest Other large tree species, of less common occurrence, will be considered later

In the area cut over, referred to above, only the conifers had been removed, leaving the two principal deciduous species standing, as shown in Plate III This gave an opportunity to estimate the relative distribution and character of the latter An estimate was also made of the comparative number of species in the forest having a diameter not less than 1 5 dm This was done by listing the individuals in a belt transect 220 m long and 10 m wide It resulted in the following data so far as the principal species are concerned hemlock, 80 5 per cent, maple, 13 5 per cent, yellow birch, 4 5 per cent, basswood, 1 5 per cent

On entering the forest one is impressed with the apparent age and maturity of the trees (Pl IV) The light is much reduced by the dense canopy above, formed principally by the fine spray of the hemlocks An examination over a large area shows considerable diversity in regard to light conditions, the differences are due to more or less open areas caused by windfalls of varying ages In reality, the forest may be considered as a patchwork of these windfalls, which are ever appearing, maturing their growth and consequently producing a general shift in the position of the better lighted areas

The forest floor is rather uneven and on the whole well drained, with the general direction of the gullies north (toward Lake Superior) A few of these gullies are occupied by small streams, even during the summer months, others contain no running water, but are very moist, so that the moisture content of the soil is quite variable for different portions of the forest This seems to be the controlling factor in causing certain departures from the ordinary composition of the forest (Pl V)

There is comparatively little shrubby vegetation in the dense hemlock forest Of the few shrubs found, probably *Lonicera canadensis* Marsh (bush honeysuckle) is the most shade-tolerant The most important ecologically is *Rubus parviflorus* Nutt (salmon berry), which is quick to appear where an opening admits even a slight increase of light to the forest floor The bottoms of shallow draws are sometimes covered with it, even when partially shaded Large numbers of woody sugar maple seedlings from 2 to 6 dm tall often form a shrubby growth of considerable ecological importance Other shrubs and shrubby trees found more or less frequently in or near the border of windfall areas are *Acer spicatum* Lam (mountain maple), *Amelanchier canadensis* (L) Medic (shadbush), *Salix rostrata* Richards (Bebb's willow), *Prunus virginiana* L (choke cherry), *Cornus alternifolia* L f (alternate-leaved dogwood) and *Corylus rostrata* Ait (beaked hazelnut)

In general, the herbaceous vegetation forms a closer index to the moisture content of the surface soil than the woody vegetation The most widely spread and shade-tolerant species of the hemlock forest is *Aralia nudicaulis* L (wild sarsaparilla) Others of rather general distribution are *Galium triflorum* Michx (bedstraw), *Aster macrophyllus* L (large-leaved aster), *Clintonia borealis* (Ait) Raf , *Mitchella repens* L (partridge-berry), *Oxalis Acetosella* L (wood sorrel), *Trientalis americana* (Pers) Pursh (star-flower), *Lycopodium annotinum* L (stiff club moss) and *Aspidium spinulosum* (O F Müller) Sw var *intermedium* (Muhl) D C Eaton The following list is not so characteristic, but it includes some species which are frequently found along water courses or low ground *Asplenium Filix-femina* (L) Bernh (lady fern), *Onoclea Struthiopteris* (L) Hoffm (ostrich fern), *Phegopteris polypodioides* Fée (beech fern), *Circaea alpina* L (enchanter's nightshade), *Solidago latifolia* L (broad-leaved golden-rod), *Mitella nuda* L (bishop's cap), *Streptopus roseus* Michx (twisted-stalk), *Cornus canadensis* L (dwarf cornel), *Chimaphila umbellata* (L) Nutt (pipsissewa), *Prenanthes alba* L (rattlesnake-root), *Aster paniculatus* Lam , *Ranunculus recurvatus* Poir (hooked crowfoot)

Several species of mosses and lichens lend color to the general aspect of the forest One of the most conspicuous is *Neckera* *pennata* (L) Hedw , forming green mats on the sides of the trees and often extending several meters up On rotting logs in windfalls and along small creeks occur such moss species as *Brachythecium salebrosum* (Hoffm) Br & Sch , *Plagiothecium turfaceum* Lindb , *Hypnum Crista-castrensis* L and the lichen *Lobaria pulmonaria* (L) Hoffm

II Composition and Dynamics of the Forest

As before indicated, one of the major problems in connection with the forest of the north slope is to account for its composition, especially as regards the relation between the hemlock and maple As one ascends the slope the maple contingent becomes greater and the hemlock less, so that finally there appears to be at first sight an almost pure stand of maple (Pl VI)

The fact that the most conspicuous stand of almost pure hemlock forest is to be found on the north slope of the first range within about 1000 m of the shore is probably to be accounted for by climatic conditions, rather than by differences in character of soil The present composition of the hemlock climax has undoubtedly existed for centuries In other words, the forest as a whole is in equilibrium as regards the relative numbers of the component tree species at a given altitude A casual observation of the stages of succession in a windfall area might lead one to think that maple should be the predominant tree (Pl VII, Fig 1) For this reason it seemed necessary to consider carefully such questions as the rate of growth, habit, shade tolerance, etc , of the more important species, and the relationships of their development, as shown by quadrat studies

1 Consideration of individual species

Tsuga canadensis (hemlock) — This species continues to grow in diameter many years after its top has reached the crown of the forest, with the result that the stand consists of individuals with great diversity in their ages Sapling stages are quite common, though their growth is often very slow The tolerance of all stages for weak light explains the dominance of the species over maple, its nearest competitor in the forest On account of this tolerance, suppression at some stage of its earlier growth is the rule rather than the exception

The tree usually seeds at intervals of every two or three years, and, in spite of reduced fertility, many more seedlings start than are able to mature, even though they are not noticeably abundant, as in the case of the maple The production of seeds and seedlings is, therefore, not the critical factor in the regeneration of either species

The species is extremely sensitive to sudden changes in the density of the forest, and seedlings respond quickly in rate of growth to slight increases in the amount of light admitted, but they cannot endure open situations, and, therefore, the tree will not take a central position in an open windfall unless it is sheltered by faster growing species On account of its shallow root-system, it is very susceptible to surface fires

Acer saccharum (sugar maple) — This species, as it occurs in the hemlock climax, is tall and slim and free of limbs except near the top The trees are apparently healthy, though all of them have undoubtedly suffered more or less suppression As already noted, the seedlings occur in such numbers that a superficial observation might lead one to conclude that in a few generations the forest would become a pure stand of maple (Pl VII, Fig 2) Closer observation soon shows that a very small percentage of these ever mature According to Frothingham (15), the trees seed in three to five years under forest conditions, and even-aged groups of very close-standing seedlings are of common occurrence They prefer maple leaf mold and avoid areas covered with hemlock needles The close and abundant growth of the seedlings results in such severe competition that the individuals are weakened and most of them succumb to suppression or disease The seedlings, however, are very tolerant of shade conditions, and a few here and there are able to persist and take advantage of the increased light occasioned by a windfall Indeed, the relative stand of maple and other hardwoods in the hemlock climax seems mainly to be conditioned by the number of windfall areas In such areas, *Rubus parviflorus* often forms a ground-cover, affording more or less protection to young seedlings which are exposed to strong sunlight

Betula lutea (yellow birch). — This tree, coming next to maple in its distribution, is an important element in the climax formation. In the forest it becomes slim and tall with a clean bole, having limbs only near the top. A specimen was observed along a wooded road about 30 m. tall, with a broad crown occupying half the height; this tree was 5.6 dm. in diameter and was fruiting heavily. It grows more rapidly than the maple and in its earlier stages requires much more light. Seedlings are comparatively rare in the hemlock forest; when found, they are likely to occur in well-lighted windfalls. Sometimes they are very numerous on a small area in full sunlight. They occur also on rotting logs with hemlock and other seedlings, and are apparently free from disease. The natural place of regeneration for the species is in windfall areas. Where an area has been slightly burned over, the seedlings are sometimes very numerous. At one point, where the forest had been cut away, the mature specimens of birch seemed more prone to rot than the maple, apparently suffering from a sudden influx of bright sunlight; in other words, in most of its stages maple seems to be a less critical tree than the birch. The latter is a much less aggressive reproducer than the maple, in spite of the fact that it seeds more often. It may and often does become *extensive* in its habit (Frothingham, 15), producing large stands of even-aged trees, which shows that its seed production has a high enough "factor of safety" to be well within the limits required by nature. Besides reproduction by seeds, this species readily sprouts from the stump. It seems clear that its relative distribution in the hemlock climax is not based on the performance of its seeds, but on its less tolerance for shade conditions than the maple and hemlock.

Other species of trees in the hemlock forest. — Several other tree species occur, but they are of less importance ecologically than those mentioned. One of these of occasional occurrence is basswood (*Tilia americana* L.), a member of the deciduous climax. It grows to be a large tree, with a clear bole nearly up to the forest crown. Seedlings were frequently found having a distinctly prostrate habit; the leaves become very large in the shade. *Thuja occidentalis* L. (arbor vitae) occurs in low spots, but is not a tree of general distribution As a forest tree it often becomes very large Its presence along the shore-line will be discussed later *Pinus Strobus* L (white pine) is occasionally found as a very large tree, towering above the rest of the forest As regards distribution, it is considered a member of the pine-hemlock climax of Clements (5) My observations seemed to indicate that where one was found, several others were likely to occur in the same neighborhood *Abies balsamea* (L) Mill. (balsam) is not common It is rarely found as a mature tree in the hemlock forest, though seedlings are often frequent in windfall openings, and occasionally colonies of young trees are found in like situations Whether this species will mature in competition with others evidently depends on the size of the forest opening, in most places it is suppressed by the more shade-tolerant trees When it occurs as a mature tree in the forest, it is safe to infer that the opening was well lighted for a considerable length of time Its behavior in this respect bears out the findings of Cooper (6) on Isle Royale, where he showed that the birth-rate of this species is balanced by a high rate of mortality when in competition with certain other species

Other tree species occasionally found in the hemlock climax are *Picea canadensis* (Mill) BSP (white spruce), *Quercus rubra* L (red oak), *Fraxinus americana* L (white ash) and *Ostrya virginiana* (Mill) K Koch (hop hornbeam)

2 Quadrat studies

The method of quadrat studies was found useful in connection with the study of forest regeneration and the distribution of the principal species Where it became necessary to determine the average ages of the trees, this was done by means of tables prepared by Frothingham (15) The trees were too large to make felling practicable for this work. In addition to quadrat studies every other means that suggested itself was used for gaining a knowledge of the dynamics of the forest. The quadrats were 10 m square

Quadrat 1 (Fig 3) — This quadrat shows the distribution of trees in the typical hemlock climax reproduced in Plate IV It represents a condition of mature growth Most of the trees here stand at an average distance of from 2 to 3 m It is noticeable, however, that practically half of this quadrat is occupied by a giant hemlock 300 years old, whose sphere of influence has undoubtedly extended much farther than the younger trees The forest floor here was free of large shrubs, of small woody plants,

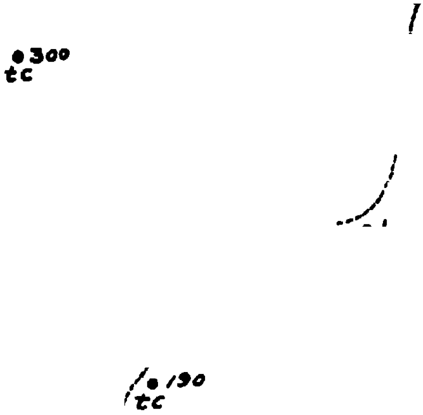


Fig 3 Quadrat 1, which is 10 meters square (see Plate IV for location) The numerals indicate the approximate ages of the trees Demarcation between old and young growth shown by dotted line *ta* = *Tilia americana* *tc* = *Tsuga canadensis*

50 specimens of *Rubus parviflorus* were counted, 14 of *Lonicera canadensis* and at least 300 seedlings of *Acer saccharum* The most conspicuous herbaceous plant was *Aralia nudicaulis* Other herbaceous plants noted were *Phegopteris Dryopteris*, *Clintonia borealis*, *Galium triflorum*, *Mitchella repens*, *Mitella nuda*, *Cornus canadensis* and *Lycopodium annotinum* In fact, both the woody

and herbaceous vegetation was typical of a well-drained portion of the dense hemlock forest

Quadrat 2 (Fig 4) — This was taken in a windfall It consists of comparatively young growth The oldest standing specimens consist of a hemlock 130 years old, a white spruce 110, and a sugar maple 90 years old; and none of these had reached their full growth The dominating influence of this hemlock is clearly shown in the diagram Its dense spray is more effective in causing suppression than that of the maple or even of the white spruce The best-lighted area of the quadrat is occupied by the younger growth, nearly one third of which consists of balsam The maple, 100 years old, shown near the top of the quadrat, was broken off

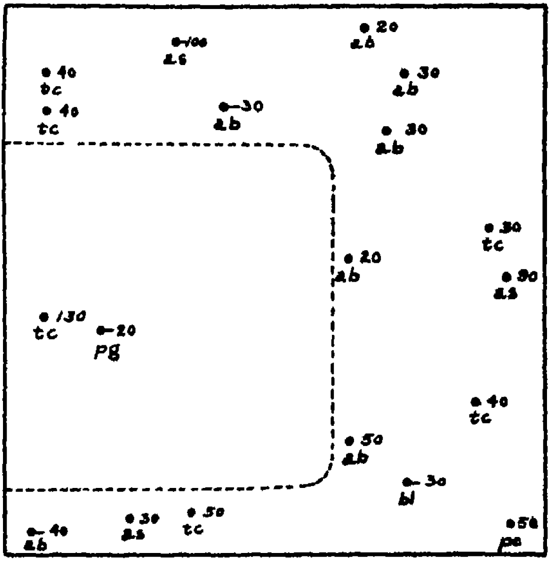


FIG 4 *ab* = *Abies balsamea*, *as* = *Acer saccharum*, *bl* = *Betula lutea* *pc* = *Picea canadensis*, *pg* = *Populus grandidentata*, *tc* = *Tsuga canadensis*, •— = fallen tree Numerals indicate the approximate ages of the trees several feet above the base by a secondary windfall, and in falling apparently leveled four other trees as shown, consisting of two balsams, a yellow birch and a specimen of large-toothed aspen (*Populus grandidentata*) The last three species named are all faster growing than hemlock or maple Of the 14 trees which are standing, 5 are balsams, 5 hemlocks, 2 maples and 1 white spruce The oldest balsam is 50 years, and it is certain the other balsams will be suppressed, probably before any one of them reaches 100 years White spruce (*Picea canadensis*) is very rare in the hemlock forest, and it is likely that this single specimen will eventually disappear before the maturing hemlocks This leaves the struggle between the 5 hemlocks and the 2 maples and typifies the final stage in any windfall It is very suggestive in the light it sheds on the ultimate composition of the forest at this point

Salmonberry and large seedlings of mountain maple and sugar maple formed a low woody growth that acted as a screen for the usual herbaceous vegetation The quadrat contained several hundred sugar maple seedlings, the oldest being about 5 years old The latter were very much affected by anthracnose leaf-spot and by an insect disease Ninety hemlock seedlings were counted, most of them growing on rotting logs in the shadier part of the quadrat Large-toothed aspen was represented by 15 seedlings, the largest individuals, though only 3 years old, were twice as tall as the 5-year seedlings of sugar maple Balsam seedlings were found in the sunnier parts of the quadrat, 25 individuals being counted Several species of mosses, already mentioned, were found on rotting logs in or near this quadrat They are often of considerable ecological importance in the formation of seed beds

In the quadrat studies above described, certain conclusions in regard to shade tolerance and its effect in the distribution of the species seem inevitable This will be considered in what follows

3 Initial physical factors and competition

It is evident that a great many factors enter into the dynamics of the forest A few of these have been pointed out as they affect the life-history and occurrence of the dominant species of trees In a consideration of the composition of the hemlock climax on the north slope two questions arise first, What causes the variation in composition from the base of the slope to the top of the ridge, a difference in elevation of approximately 300 m ? second, What is the most effective factor governing the composition at any one point? Frothingham has pointed out that there are two sets of factors influencing the distribution and dominance of trees in the natural forest, namely, *physical*, including soil, humidity, light, etc , and *physiological* (biotic), including aggressiveness in reproduction, tolerance of shade, rate of growth, form, size, longevity and resistance to injury and disease The first question seems to be answered by a consideration of the physical factors of moisture and light Soil evidently has little to do with it, if all the hemlocks were removed from the north slope, maple could easily take possession, as is evident from its regeneration in windfalls and its prominence in the ranges farther south Hemlock, rather than maple, is thus the critical tree on the north side of the first range This species is known to prefer cool, moist slopes, where the drainage is fair Good drainage, however, may be left out of consideration here, as it occurs on the ranges farther south where hemlock is not prominent The greatest humidity lies low along the lake shore Here dense fogs are frequent even in the earlier part of the growing season The smaller relative humidity at the higher elevations allows a corresponding increase in the intensity of the light near the top of the ridge As before noted, hemlock is known to be very sensitive in its response to light, it is also known to be more shade-tolerant than maple Thus it seems clear that the dominance of hemlock at lower elevations on the north slope and its absence as a dense stand on higher elevations and on the ranges farther south are correlated with the physical factors of moisture and light

The answer to the second question involves the consideration of the relative physiological response of other species, especially maple and yellow birch, to the conditions imposed by the dominant hemlock Hemlock and sugar maple are the most conspicuous examples in the Lake region of what Frothingham calls *intensive* reproducers, i e , species which are more aggressive inside than outside the forest The effective aggressiveness of each species is due to a combination of factors Both species, when growing under forest conditions, are likely to have a suppressed period of growth for at least the first 50 years Quadrat studies show a great variation in age of individuals, even among the adult trees forming the forest crown, mature trees varying from 100 to 300 years or more The age of one hemlock, measuring about 1 m in diameter, was estimated at over 400 years The greatest tolerance of maple, however, seems to be in the seedling stage, quadrat studies often show hundreds of seedlings in the dense shade of the hemlocks On the other hand, the seedlings of hemlock appear rather critical in their light requirements In general, they grow more abundantly in the more open part of the forest, but not necessarily in a windfall

4 Equilibrium at any point

Though the different tree species vary widely in their relative production of seeds and seedlings, it seems certain that all are productive enough to be well within the limits required by nature It has been pointed out by various observers that the "factor of safety" in seed and seedling production is very large and that there is an enormous wastage in all cases While this larger seed production may be important on denuded areas, it seems clear that it has little to do with the relative number of individuals of different species, where the dominant species are intensive and where a balance has long been reached and maintained This balance is changed little if any by excessive seed production of any species It is conditioned by something more invariable than seed production. The true explanation seems to be the competition between the species under the conditions imposed by the physical factors at that point For example, the population of the yellow birch, which forms approximately 5 per cent of the total tree population half-way up the north slope, is a measure of its relative response to the conditions imposed by the hemlock and maple Since the equilibrium of the forest represents the result of the effective response of each species, the balance may be shown diagrammatically as in Figure 5 The vectors DA, AB and BC (upper figure) illustrate the effective response of the three principal species somewhere up the north slope Evidently the magnitude of the vectors does not correspond to the number of individuals of each species, in other words, while population may indicate response, it is not a measure of it The vector CD indicates the effective control of all other species. The lower figure illustrates the conditions of balance near the top of the ridge If any one species were eliminated from the forest, it would eventually come back in approximately the same proportion at any point

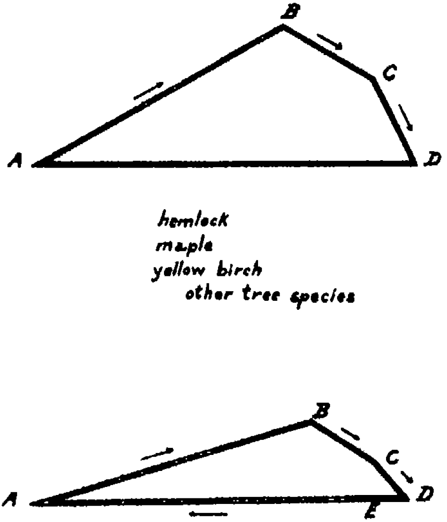


Fig 5 Vector diagrams, illustrating approximate equilibrium at two points on the north slope of the first range The upper figure illustrates the conditions half-way up the slope, the lower figure shows conditions of balance near the top, hemlock has been nearly replaced by maple, *CD* is represented largely by basswood and ironwood

III Successions Leading to the Hemlock Climax

1 Primary successions

The primary successions leading to the hemlock climax may be seen along the shore of Lake Superior, at the foot of the first range The pioneer stages are present in most cases, but the transition is often rather abrupt Lack of well-marked zonation is probably due to the severe conditions along the shore

a) Physiographic influences

The development of the shore-line is correlated with the post-glacial history of the Lake Superior region On account of the gradual withdrawal of the lake, more and more of the north slope of the first range has been uncovered This has probably been counterbalanced to a certain extent by erosion and by the sinking of the coast in this region, which is believed to be taking place (1)

The rock shore is the predominant type Where it is gravelly or sandy, a little investigation shows that the rock is not far underneath The exposed rock is largely red sandstone, dipping everywhere at an angle, as shown in Plate VIII, Figure 1 In places conglomerate is exposed and loose boulders along the shore are frequent The width of the rock beach varies from 15 to 45 m Sandy or gravelly beaches in more or less protected places may be narrower than this, so that the forest comes comparatively close to the water, as seen in Plate VIII, Figure 2, which shows a narrow gravel beach

There is such a variation in the slope and character of the rocky shore that it is difficult to divide it into any definite zones in accordance with the ecological factors influencing plant life Its lower portion, being always subject to wave action during both summer and winter, is devoid of plant life, except in sheltered corners of the rocks which escape the direct pounding of the water The lower limit of plant life is marked, roughly, by the maximum height of the waves in summer The winter waves and ice usually reach much higher than this, and thus mark out the upper limits of a zone in which only the hardiest perennials are able to survive

b) The shore successions

Since the surface of the lake has been at the present level for a long period of time, the distribution of the pioneer associations at any point along the shore has reached a balance which will remain practically the same so long as the climatic, ecological and historical factors remain unchanged In other words, it is probably incorrect to say that active invasion or retrogression is taking place at the present time, even admitting the slight changes in coast line due to subsidence or erosion.

The pioneer associations along the shore are composed of crevice plants, of lichens and of mosses (Pls IX–X) On account of the fragmental nature of the rocks, crevice plants appear to be the most important pioneers, most of them are perennials The seeds lodge in the moist cracks of joint and bedding planes, and germinate even where little or no soil is present Gradually enough soil collects around the seedling for the establishment of a firm root-system, and then it is able to persist for many years and spread by means of offshoots Two of the commonest and hardiest species in this connection are *Juncus Dudleyi* Wiegand and *Deschampsia caespitosa* (L) Beauv (hairgrass) The former was found within 3 dm of the water, the latter is undoubtedly the commonest grass growing in the crevices of the shore rocks

Plate VIII, Figure 1, represents a typical situation for crevice vegetation Such a habitat enables even woody plants to come in very early In the foreground is shown a large specimen of ninebark (*Physocarpus opulifolius*) and in the background a small specimen of mountain ash (*Pyrus sitchensis*) The former has assumed more or less of the *krummholz* form of growth, especially on the lake or windward side, its habit of growth thus makes it more efficient as a conserver of soil and moisture

The rate of succession along the outer shore is evidently not to be measured by the character of the plant life, the highest forms being found with the lowest As before indicated, this rate is exceedingly slow, owing to the severity of the situation In spite of this, a large number of species are found. One group may be classed as typical crevice plants Among these, besides those mentioned, are *Campanula rotundifolia* L (bluebell), *Aster Faxoni* Porter, *Senecio Balsamitae* Muhl (groundsel), *Fragaria virginiana* Duchesne (strawberry), *Achillea Millefolium* L (yarrow), *Equisetum arvense* L (horsetail)

In the outer portion of the shore-line at least, shrubs often occupy the most exposed situations The typical species are *Physocarpus opulifolius* (L) Maxim (ninebark), *Rosa acicularis* Lindl var *Bourgeauiana* Crépin (wild rose), *Salix petiolaris* Sm and *Cornus stolonifera* Michx (red-osier dogwood) The seedlings of *Populus tremuloides* often accompany the willows Along the inner portion of the shore (Pl XI), tree seedlings are frequent, the commonest of which are those of *Thuja occidentalis* L Here the usual successions occur, with lichens and mosses as pioneers With a few exceptions, they are well above the wash of the winter waves The wash of the higher water can often be very accurately traced on large isolated boulders of conglomerate On account of its differential weathering, this material supports a richer flora of lichens and mosses than the sandstone, and the transition from washed to unwashed surface often appears rather abrupt

Several species of lichens and mosses occur in the severest situations The pioneer crustose lichen appears to be *Rhizocarpon petraeum* (Wulf) Koerb This form persists often under the lash of the winter waves Other crustose forms common on the rock farther back are *Placodium aurellum* (Hoffm) Tuck and *Lecanora cinerea* (L) Sommerf A few species of mosses, such as *Ceratodon purpureus* (L) Brid, *Leptobryum pyriforme* (L) Wils and *Funaria hygrometrica* (L) Sibth, occur in exposed crevices In some places they undoubtedly pave the way for higher plants Farther inshore, various foliose and fruticose lichens and mat-forming mosses make a definite stage of the rock succession Among these may be mentioned *Grimmia apocarpa* (L) Hedw, *Amblystegium varium* (Hedw) Lindb, *Lobaria laciniata* (Huds.) Wainio, *Parmelia conspersa* (Ehrh) Ach, *Stereocaulon paschale* (L) Fr and various species of Cladonia

Following the mosses and lichens one often finds the bearberry (*Arctostaphylos Uva-ursi* (L) Spreng) as a pioneer mat-former

With the accumulation of more soil, shrubby species become more abundant Besides those mentioned, the following occur *Diervilla Lonicera* Mill (bush honeysuckle), *Amelanchier canadensis* (L) Medic (shad bush), *Cornus alternifolia* L f and *Rubus parviflorus* Nutt (salmonberry)

In the development of this succession finally come the trees, the roots of which sometimes spread 3–10 m before finding a suitable crevice for anchorage (Pl XII) Roots of this kind form an important barrier for holding back soil washed from above The fallen trunks also assist in the same manner, as well as finally furnishing additional humus by their decay

c) Types of shore

The character of the shore vegetation is largely influenced by variations in physiography This includes submerged ledges of rock, shore, cliffs, coves and the accumulation of shingle barriers (see Pl XIII, Fig 1) Submerged ledges breaking the effect of the waves and coves affording protected areas are both factors in extending the forested area closer to the water's edge The effect of these two influences may be seen in Plate VIII, Figure 2

It seemed possible to classify the shore into three general types, as shown in Figure 6 Figure *A* shows a type in which the surface immediately back of the shore-line is low It often represents the mouth of a gully, and possibly of a drowned river (see Ruthven, 25, p 25) The area is swampy, usually being occupied by large specimens of *Thuja occidentalis* and *Fraxinus nigra* It is sometimes separated from the immediate shore-line by a narrow zone of shingle and driftwood Back of the area there is often an abrupt rise of from 6 to 10 m to the typical hemlock forest

In *B* the hemlock forest extends practically up to the shore-line, though there is always a fringe of other species on the immediate outskirts, the commonest being arbor vitae and white birch Other species that occur are *Abies balsamea*, *Acer saccharum* and *Acer spicatum* Stages intermediate between *A* and *B* occur

The third type, *C*, represents the conditions where the shore-line is bordered by a rocky cliff In this case the area above is often forested to the very edge of the cliff On account of the dip of the strata, such areas are so well drained that the vegetation becomes xeric in character This was found to be true even where the soil was 3 dm deep, as was observed at one point At this point the ridge had once been covered by a growth of pine, which had been blown down and was being followed by a growth of white birch, aspen and balsam, the two former being on the lake side and better able to adapt themselves to the unusually severe wind conditions

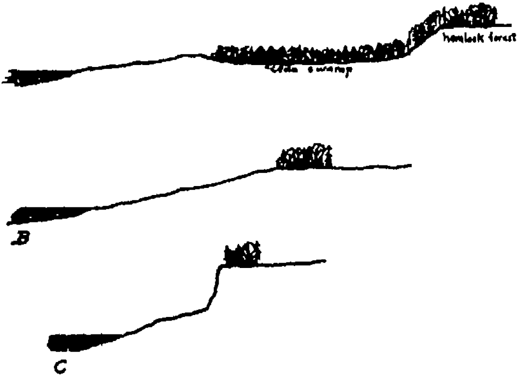


FIG 6. Types of shore-line, see text, p 34

2 Secondary successions in the hemlock climax

In the latter part of the summer of 1919 an extensive fire swept over a portion of the north range, destroying several square miles of virgin hemlock forest This fire extended as far east as the range line between townships 42 and 43 The conifers were killed outright, though many dead trunks were left standing (Pl XIII, Fig 2) It was very evident that the deciduous trees, including the sugar maple and especially basswood, were more resistant to the effects of the fire than the conifers This was especially noticeable in the zone between the burned and unburned areas, where the trees were singed Plate XIII, Figure 2, shows how thoroughly the humus was burned off, exposing what appears to be ordinary talus material, composed of angular, unwashed fragments of sandstone, mostly 1–3 dm in diameter

"Burn" associations had started over the entire area, being farther advanced at some points than at others The commonest herbaceous pioneers consisted of *Erigeron canadensis* L (horseweed), *Epilobium angustifolium* L (great willow-herb), *Aster macrophyllus* L, *Aralia hispida* Vent (bristly sarsaparilla) and *Polygonum Douglasii* Greene Amongst the shrubby species coming in next the following were noted *Rubus parviflorus* (salmonberry), *Sambucus racemosa* L (red-berried elder), *Diervilla Lonicera* Mill (bush honeysuckle), *Rhus typhina* L (staghorn sumac) and *Rubus idaeus* L var *aculeatissimus* (C A Mey) Regel & Tiling These are followed by *Prunus pennsylvanica* L f (wild red cherry), *Acer spicatum* Lam (mountain maple), seedling aspens and occasional seedlings of sugar maple (*Acer saccharum*) Hemlock seedlings undoubtedly come in at a later stage, finally displacing the maple One of the most noticeable elements of this secondary succession is *Rubus parviflorus* The plant spreads rapidly over large areas by stems just below the surface, which are sometimes several meters long The foliage forms a "leaf mosaic" which reduces the light to such an extent that shade-tolerant species are able to make an early start, thus probably hastening the climax stage

B THE MAPLE CLIMAX

This is the climax associated with vegetational development at the top of the first range and over the ranges farther south Its mature form may be seen 100 m north of the summit of the range (Pl VI) Here a 10-meter quadrat was laid out (Fig 7) It represents a stand of almost pure maple The larger trees averaged about 4 m apart, the forest canopy being rather dense for maple The uniformity in the ages of several of the younger trees marked them out as the survivors of a single generation of seedlings In fact, the presence of several dead saplings varying from 30 to 40 years of age suggested that these trees had already reached a critical period in their development Thrifty specimens of Tilia and Ostrya were found just outside the limits of the quadrat The soil at this point was a rich leaf mold of medium acidity It was not deep, as indicated by the root-systems of fallen trees, exposing the bare rock Though the forest floor was comparatively open, immature shrubby vegetation was represented by

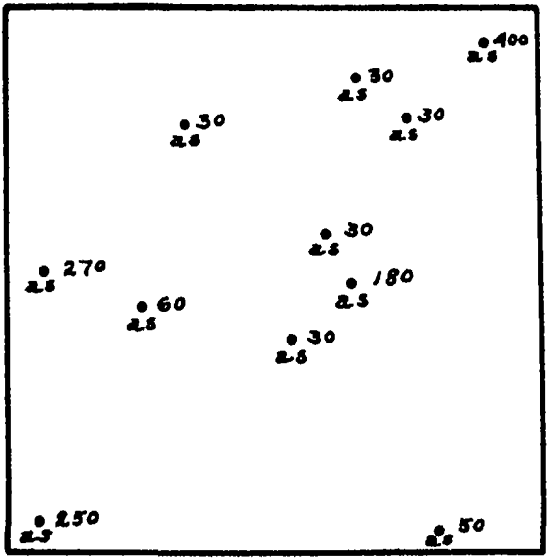


FIG 7 Quadrat 3, representing a stand of trees in a forest of almost pure maple, taken in Section 14 about 100 meters from summit of ridge (see Pl VI) *as* = *Acer saccharum*

specimens of *Rubus parviflorus* and *Sambucus racemosa* The latter species gets to be very large in maple windfalls, dominating the ground-cover The following are typical herbaceous species *Aspidium spinulosum* (O F Müller) Sw var *intermedium* (Muhl) D C Eaton, *Phegopteris Dryopteris* (L) Fée (oak fern), *Adiantum pedatum* L (maidenhair), *Botrychium virginianum* (L) Sw (rattlesnake fern), *Hystrix patula* Moench (bottle-brush grass), *Milium* *effusum* L (millet grass), *Solidago latifolia* L (broad-leaved goldenrod), *Ribes Cynosbati* L (wild gooseberry), *Smilacina racemosa* (L) Desf (false spikenard), *Actaea alba* (L) Mill (white baneberry), *Viola canadensis* L , *Sanguinaria canadensis* L (bloodroot), *Aralia nudicaulis* L (wild sarsaparilla), *Polygonatum biflorum* (Walt) Ell (small Solomon's seal) and *Galium triflorum* Michx (bedstraw) The last species is one of the commonest of the smaller ground-covers

The maple climax, as above described, occupies a comparatively narrow zone on the north side of the first range As will be shown later its development on the south side is as yet in the early stages, being closely related to the physiographic features of the range and the adjoining valley of Carp River

I General Physiographic Features

That the top of the first range still holds out against the mesic forest is undoubtedly due to the peculiar topography of this range As is evident from Figure 2, this topography is associated with the geological formation of Carp Lake, which was once much larger than at present The dip of the strata toward the north has created a great cliff or escarpment, which is continually weathering away producing a talus slope at its foot (Pl XIV, Fig 1) This cliff extends west and west-southwest across T 51 N , R 43 W , a distance of about 10 km (Map 2) It varies from point to point along the range in elevation of summit, height of escarpment and width of talus slope At one point opposite Carp Lake the talus descends into the lake, but at most points there is a fringe of forest between the foot of the talus and flood-plain of the river, as shown in Plate XIV, Figure 1 In Section 14, there is a depression in the cliff where the escarpment has entirely disappeared, leaving a *saddle* across the range The same condition, though less marked, occurs about a mile west in Section 15, and in varying degrees at other points along the range, making it possible at such places to descend into the valley without difficulty Where a saddle is sufficiently low, as in Section 14, the talus is almost entirely covered by soil washed from above, and the fringe of forest from below may extend clear across the depression. In Section 15 this process has not gone so far (Pl XIV, Fig 2) There is still a rock face varying from 3 to 5 m high The relation between the various physiographic features as they appear at different points along the range is shown in Figure 8

Cross-section *A* (Fig 8) represents a stage of the cliff found opposite Carp Lake in Section 22 Here the escarpment is high and the talus slope dips into the lake At this point the trap and sandstone portions of the cliff can be readily distinguished The trap is superimposed upon the sandstone and has undergone a greater disintegration, forming a ledge as shown Cross-sections *B* and *C* typify ordinary conditions where the escarpment is high and the talus slope from 200 to 300 m wide, bordered by a more or less mesic forest at the foot At *D* is shown a stage where the top has been rounded off to such an extent that xeric tree species, such as red and white pine, are able to gain a footing The latter is usually more abundant under the brow of the cliff, where it is more or less sheltered The former is found in the more exposed situations, being the first to creep over the top when conditions become favorable Stages *B*, *C* and *D* may all be seen in Section 14 Cross-sections *E* and *F* represent stages at a low point in the range,

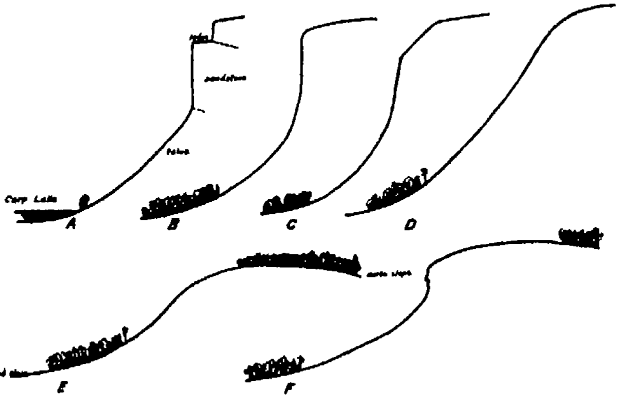


Fig 8. Typical cross-sections at various points through summit of first range

such as is shown in Plate XIV, Figure 2, preceding the formation of a saddle Here the talus slope is much reduced and the forest pushes well up toward the summit, even though the latter may still remain xeric

II Successional Relations

1 Xerarch successions on the first range

An ecological survey of the vegetation involves an examination of the environmental factors and plant successions (1) at the summit, (2) along the escarpment, (3) on the talus slope, and (4) below the talus slope

a) Summit of the range

(1) Ecological factors

In general, the forested area of the north slope may fall short of reaching the crest of the ridge, as shown in Figure 8 *F*, or may reach slightly over the summit, as at *E* From this point to the brink of the precipitous cliff, which averages from 20 to 40 m, there is usually a large amount of bare rock surface Where the soil has accumulated, it is of very slight depth There seem to be two principal reasons for this condition, both due to the presence of the escarpment (1) the soil from rock disintegration is washed over the south side of the crest nearly as fast as it is formed, (2) the escarpment itself forms an effectual barrier to the encroachment of the mesic forest below This zone of bare or nearly bare rock surface therefore remains unprotected Its exposed situation makes it especially susceptible to the dynamics of weathering, including the frost of winter, the heat of summer, full exposure to rain and to all winds from the south A portion of the soil washed over the crest accumulates in a narrow strip along the top of the talus slope The rest is gradually washed down through the talus, finally reaching the forested area at its foot On the other hand, soil found north of the crest is soon checked in its descent by the forest A certain amount of it collects in depressions and irregularities of the rock surface and along the edges of joint planes, affording a foothold for crevice plants and matted vegetation

(2) The plant associes

The pioneer stages at the summit consist of lichens and mosses on the bare rock surface and on the ground Among the commoner crustose lichens appear such forms as *Lecanora cinerea*, *Rhizocarpon petraeum* and *Placodium aurellum* Following these come foliose species, of which *Parmelia conspersa* (Ehrh) Ach is the most conspicuous and covers a large proportion of the rock surface, *Physcia obscura* (Ehrh) Nyl , *Lecanora garovaglii* and *Gyrophora hyperborea* Ach are less common Where a slight amount of soil has accumulated on the rock surfaces, fruticose types appear, common species being *Cladonia rangiferina* (L) Web , *Cladonia sylvatica* (L) Hoffm and *Stereocaulon paschale* (L) Fr

Associated with the lichens in the pioneer rock associes are moss species, such as *Grimmia apocarpa*, *Polytrichum piliferum* Schreb and *Tortella tortuosa* (L) Limpr , the two latter being the commonest One of the early mat-formers is *Selaginella rupestris* (L) Spreng , which often covers large areas on the rock surface It is not uncommon to find superposed upon the mat the two common mosses already mentioned The Selaginella mat becomes nearly 1 dm thick in places, living plants grow on the dead mat of former generations This paves the way for herbaceous plants (Pl XV), such as *Danthonia spicata* (L) Beauv (wild oat grass), *Potentilla tridentata* Ait (three-toothed cinquefoil), and even for woody species, such as the bearberry (*Arctostaphylos Uva-ursi* (L) Spreng) and stunted specimens (2–4 dm high) of staghorn sumac (*Rhus typhina* L) The roots of the latter creep over the rock surface for several decimeters until finally they may become anchored in a crevice Arctostaphylos is especially well adapted to the severe conditions found on these rock surfaces Often it occurs in large patches, thus aiding in the retention of more soil and the conservation of soil moisture Large angular depressions in the rock surface may occasionally be found where enough moisture is retained to support even shrubby growth without being definitely anchored in a crevice Such a case was illustrated by a low specimen (2–3 dm high) of New Jersey tea (*Ceanothus americanus* L), which had adapted itself completely to the shape of the depression, but could be pulled out bodily as a dense mat

Much of the rock at the bare summit is more or less porous in texture, rock fragments are numerous but irregular Joint and bedding planes are not so distinctly marked as on the face of the escarpment Whenever a crevice occurs, however, soil readily collects and a number of plants gain a footing The summer flora is practically a xeric one, the occurrence of certain vernal species, however, indicates that during the spring there is a comparatively large amount of moisture on the ridge, due in part, probably, to the melting snow Of the crevice plants, *Danthonia spicata*, already mentioned, is one of the more important, on account of its abundance and its densely tufted habit of growth Other noteworthy crevice plants are *Solidago randii* Britton var *monticola* Porter, *Potentilla tridentata*, *Artemisia caudata* Michx , *Woodsia ilvensis* (L) R Br , *Campanula rotundifolia* L. (harebell), *Viola arenaria* DC (sand violet), *Aquilegia canadensis* L (wild columbine), *Panicum depauperatum* Muhl and *Panicum meridionale* Ashe

Where a small amount of dry soil has accumulated, the following species occur *Antennaria neodioica* Greene (everlasting), *Lechea stricta* Leggett (pinweed), *Panicum xanthophysum* Gray, *Satureja vulgaris* (L) Fritsch (basil), *Aralia hispida* Vent (bristly sarsaparilla), *Apocynum androsaemifolium* L (spreading dogbane), *Epigaea repens* L (trailing arbutus), *Hieracium scabrum* Michx (hawkweed), *Epilobium angustifolium* L , *Aster macrophyllus* L , *Corydalis sempervirens* (L) Pers., *Cerastium arvense* L , *Fragaria vesca* L var *americana* Porter and *Carex adusta* Boott

It will be noted that these are perennial species A few annuals occur, such as *Silene antirrhina* L (sleepy catchfly), *Erigeron canadensis* L (horse-weed) and *Polygonum Douglasii* Greene These annuals lead a precarious existence, as their seeds must, in the main, be washed over the cliff each year The distribution of the herbaceous species already listed varies considerably from one point of the ridge to another Their presence results in the accumulation of humus, especially in depressions or in connection with dead mats of Selaginella

Accompanying the herbaceous vegetation are a few species of low shrubs, the commonest of which are species of blueberry (*Vaccinium pennsylvanicum* Lam var *angustifolium* (Ait) Gray) and *Vaccinium nigrum* Britton These often form large patches slightly back of the summit, where more soil has accumulated Other species found along the summit are *Juniperus communis* L var *montana* Ait , *Rosa acicularis* Lindl , *Salix humilis* Marsh , *Diervilla Lonicera* Mill , *Shepherdia canadensis* (L) Nutt and stunted specimens of shadbush (*Amelanchier canadensis* (L) Medic)

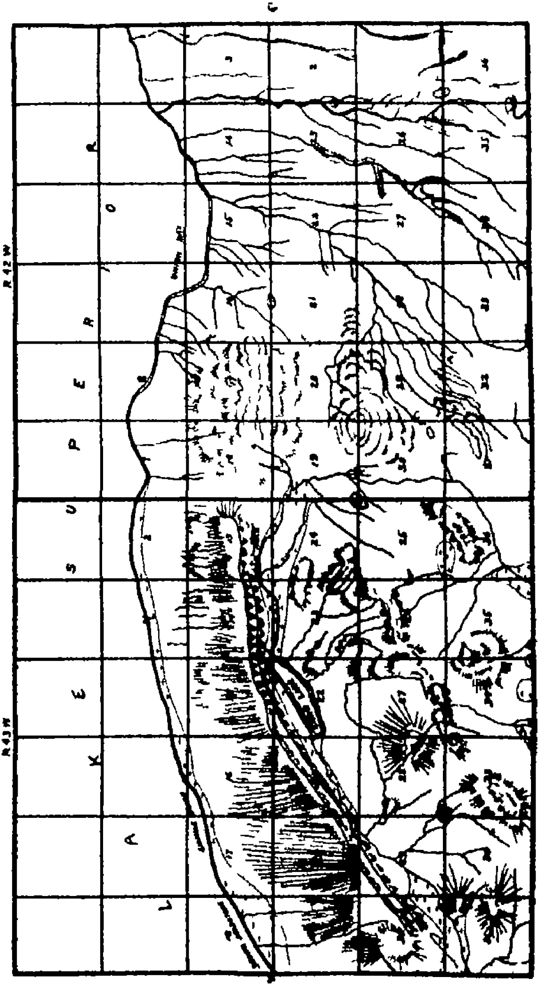
A few dwarfed specimens of white pine (*Pinus Strobus*) are scattered along the summit, but the species is much more common over the crest of the ridge (Pl XIV, Fig 1), where it receives more shelter and moisture The gray pine (*Pinus Banksiana* Lamb) was noticed at only one point

The limit of forest growth is bordered by a very distinct transitional zone all along the summit The general character of this is shown in Plate XVI, but it varies a great deal in composition at different points of the ridge, approaching more mesic conditions at lower elevations Gnarled and stunted specimens of red oak (*Quercus rubra* L) are mingled with aspen (*Populus tremuloides* Michx) and white birch (*Betula alba* L var *papyrifera* (Marsh) Spach), the latter sometimes appears in almost pure stands

(3) Quadrat studies

A detailed study of the transitional zone was made at a point in Section 14, just west of the saddle (see Map 2) This is typical of most of the ridge Beginning at the area of bare rock surface shown in Plate XVII, situated approximately 25 m back from the face of the cliff, a series of four quadrats was taken in succession, the last of which was in the mesic forest (Fig 9) These quadrats were 10 m square, making the total width of the transitional zone 40 m at this point

Quadrat 4 (Fig 10) — This was taken to include a portion of the rock surface (Pl XVII), as well as the marginal tree growth There the soil was thin and dry, with the ground sloping gently toward the south. Several small red pines (*Pinus resinosa*) repre-



MAP 2. A portion of the Porcupine Mountains

sented the typical tree growth They stood comparatively close, with small dead ones intermingled Amongst the red pines were a few small white pines and balsams *Aster macrophyllus* L formed a large proportion of the ground cover Besides this there were several other species already mentioned as typical of exposed portions of the ridge, such as *Salix humilis*, *Vaccinium spp*, *Artemisia caudata*, etc

Quadrat 5 — This typified the zone of scrubby red oaks (Pl XVIII), a characteristic belt very often following the conifers The oak growth consisted mostly of sprouts (up to 3 m high) coming from old root crowns in very shallow soil This quadrat was just north of the crest, so that the surface sloped gently toward the north The conditions, however, were still xeric, as indicated by the presence of such plants as *Aralia hispida*, *Danthonia spicata* and large patches of *Funaria hygrometrica* There were also a few scattered seedlings of aspen, white birch and sugar maple There were some evidences of burning on this quadrat, so that conditions might not have been entirely typical *Funaria hygrometrica* was found to be very common in burned areas over various parts of the region In general the oak sprouts seem to be the ecological equivalent of red pine The ground cover was much the same as in the preceding quadrat, with the exception of *Polygonum dumetorum*, a very common species along the edge of the mesic forest

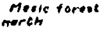


FIG 9 Transition to mesic forest (maple climax), top of ridge, at a point in Section 14, T 51 N, R 43 W, see description of Quadrats 4 and 5

Quadrat 6 — This represents a transitional stage from quadrat 5, in which the oak constituent has reached a higher stage of

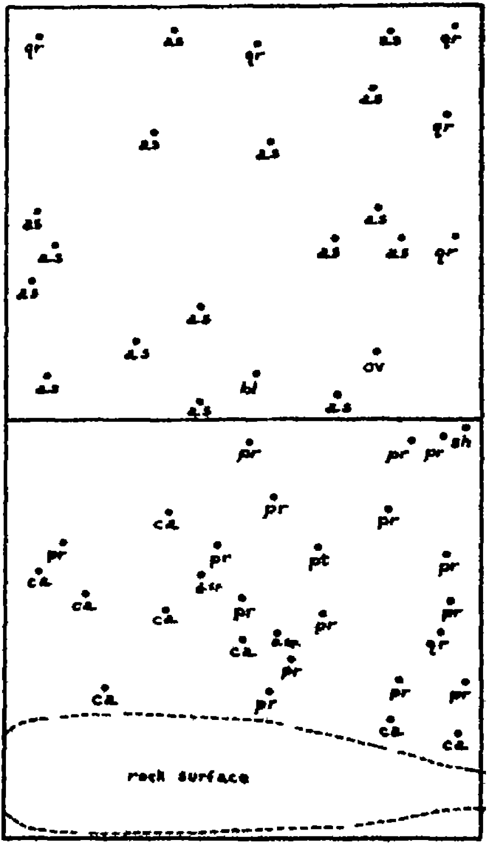


Fig 10 Quadrats 4 and 5, see Plate XVII and text *as* = *Acer saccharum*, *a sp* = *Amelanchier sp* *bl* = *Betula lutea*, *ca* = *Ceanothus americanus*, *ov* = *Ostrya virginiana*, *pr* = *Pinus resinosa*, *pt* = *Populus tremuloides*, *qr* = *Quercus rubra*, *sh* = *Salix humilis*

development, the individuals attain a height of from 7 to 10 m, with much less sprouting, though still indicating somewhat unfavorable conditions The presence of red maple and numerous sugar maple in the northern half of the quadrat indicated the transition to the mesic maple forest

Quadrat 7 — The striking feature of this quadrat was the dominance (in numbers) of sugar maple saplings 5–10 cm in diameter Intermingled with these were well-developed specimens of red oak (up to 15 m or more high), hop hornbeam (*Ostrya virginiana*) and yellow birch (*Betula lutea*)

Following quadrat 7, the maples gradually increase in size, often accompanied by basswood and a thick growth of red-berried elder (*Sambucus racemosa*), the latter disappears or becomes less frequent in the denser shade of the mesic forest farther down the slope Along the upper limit of the maple forest, it is not uncommon to see the flat, upturned root-systems of trees, especially maples, which have adapted themselves to a layer of soil not over 1 dm thick over the rock surface This area is more or less subject to windfalls, apparently not because the velocity of the wind is greater here than nearer the summit, but because it forms a critical line between the low types of trees which spread their roots out through the shallow soil, with crevice connections in many places, and the taller types which owe their increased size to a deeper, richer soil, but which offer a greater leverage to the force of the wind

This description of the transition from rocky summit to mesic forest applies in general to the higher portions of the range Variations naturally occur, depending on the elevation, exposure, local topography and depth of soil

b) The escarpment and its associes

The height of the rock face or escarpment varies at different points along the range, as shown in Plate XIV, Figure 1, and Plate XXIII, Figure 2 The upper portion may be vertical or nearly so The lower portion curves around to meet the talus slope, which is very steep at the top, or there may be a series of lower escarpments with shorter talus slopes between, as shown at the left in Plate XIV, Figure 1 Owing to the dip of the strata, the face of the cliff is always very uneven, and the seams of the rock, on account of the direction of dip, often retain a sufficient degree of moisture to support the more xeric types The unusual severity of the situation, so far as vegetation is concerned, is due to the continual splitting off of rock fragments from the parent rock

The cliff is often broken by ledges, owing to different resistances of the various kinds of rock to weathering, these may vary in width from a few decimeters to several meters, with corresponding accumulations of soil On the vertical rock faces a few species of lichens may be found, such as *Lecidea lucida* Ach , *Gyrophora vellea* (L) Ach and *Amphiloma lanuginosum* (Hoffm) Nyl The vertical face of sandstone represented in Figure 8 *A* is marked by bands of the yellow lichen, *Placodium elegans* Where ledges overhang, as shown in Plate XIX, the conditions are moister on account of the shade *Amphiloma lanuginosum* and the leafy liverwort, *Radula complanata*, are usually abundant, also various foliose and fruticose lichens, such as *Physcia obscura* (Schaer) Nyl , *Parmelia caperata* (L) Ach , *Ramalina calicaris* (L) Fr and *Gyrophora vellea* (L) Ach In the crevices of such ledges occur two characteristic fern species, namely, *Polypodium vulgare* L and *Woodsia ilvensis* (L) R Br

The flora of the exposed ledges is extremely variable On the smaller, newer ledges a few lichen species, such as *Lecidea lactea* (Flot) Schaer and *Parmelia conspersa* (Ehrh) Ach , may gain a footing On larger ledges the higher plants are usually well represented, from small herbaceous species to trees whose roots are anchored in some of the bigger crevices (Pl XX) Typical species are shown in the plate Among others may be mentioned *Potentilla tridentata, Panicum xanthophysum, Ceanothus americanus, Rubus parviflorus, Amelanchier canadensis, Polystichum Lonchitis, Thuja occidentalis* and *Juniperus communis* L var *montana* Ait

When there is a marked difference in rate of weathering between the sandstone and trap, a broad ledge 10–15 m across may be formed (Fig 8 *A*) On account of the greater deposit of soil and consequent storage of moisture, the conditions here are much more stable Such an area may develop a comparatively thick stand of pine that thrives under the protection of the cliff

The destiny of the escarpment is the condition seen where at present saddles cross the range Cutting at the top and face and filling at the bottom will continue until the lines of cut and fill meet Invasion of mesic types will be principally from below, the summit will hold out longest against the final mesic forest Plate XXI, Figure 1, shows a stage approaching such a condition

c) The talus slope

In general the width of the talus slope depends on the height of the escarpment, especially where the latter is not broken by large ledges When the face of the cliff is low, the band of talus is comparatively narrow, for here the rock fragments from above do not come in sufficient numbers to prevent invasion of the forest below Where the cliff is high, many of the larger fragments may roll 200 or 300 m , effectively checking the growth of the forest beyond this point The resulting area is desolate in appearance (Pl XXI, Fig 2), since very little vegetation gains a foothold except near the top and bottom

Where the cliff is principally sandstone, the rock fragments are smaller and more flattened than where trap predominates In the former case soil apparently collects more quickly and vegetation makes a more rapid invasion As pointed out before, there are two points on the talus where soil first begins to accumulate, namely, the bottom of the slope along the margin of the forest and the very top — at the foot of the escarpment Most of that at the top is due to fine material which is washed over from the summit and held in place This finer soil, coupled with the shadier conditions directly under the cliff, gives rise to a narrow strip of vegetation composed of a complex of species, some pioneer and some more or less mesic in character Among the more important of these are *Pinus Strobus*, *Pinus resinosa*, *Quercus rubra*, *Prunus pennsylvanica*, *Populus tremuloides*, *Ceanothus americanus*, *Psedera quinquefolia*, *Rhus Toxicodendron*, *Cornus circinata*, *Rhus typhina*, *Celastrus scandens*, *Ostrya virginiana*, *Arctostaphylos Uva-ursi* and *Symphoricarpos racemosus* Michx var *pauciflorus* Robbins This plant assemblage, especially as regards the more mesic species, is only temporary, for, as the cliff recedes, the vegetation must recede with it. As the height of the cliff becomes less, the increased light and lessened degree of moisture make conditions intolerant for the more mesic species Finally, with the disappearance of the escarpment, only xeric species are able to endure, such as occur on the more exposed portions of the smaller talus slopes

The border of the forest forms a tension line at the bottom of the talus Conditions for growth here are more favorable, not only on account of soil accumulation, but on account of the partial shade Again, the pioneer species consist of lichens, which become more abundant here than higher up on the more exposed portions of the slope By far the most conspicuous is *Parmelia conspersa*, which covers the top of nearly every fragment of rock (Pl XXII) The humus derived from this species paves the way for fruticose forms, such as *Cladonia rangiferina* (L) Web , *Cladonia sylvatica* (L) Hoffm and *Cladonia pyxidata* (L) Hoffm Following the lichens or sometimes closely associated with them are three species of mosses, namely, *Thuidium abietinum* (L) Br & Sch , *Hedwigia albicans* (Web) Lindb and *Ceratodon purpureus* (L) Brid The two fern species already mentioned, *Polypodium vulgare* and *Woodsia ilvensis*, follow the lichens and mosses They are very common along the bottom of the talus slope, where they send their roots down between the slabs. An early stage of the mesic forest may then follow directly, as shown in Plate XXI, Figure 2, where the talus is fringed by white birch The conspicuous omission of the usual mat stage here is due to the ability of the white birch to invade the talus before almost any other woody form Clumping specimens with several stems often occur on the bare talus and send their roots far down between the fragments. In such cases they form nuclei for other pioneer species. *Populus tremuloides* and *Populus grandidentata* are the pioneers along some parts of the forest front

As the cliff wears down and the talus slope becomes proportionately narrower, invasion from both the bottom and top is accelerated (Pl XXIII, Fig 1) This is partially due to the fact that less new talus is put down, a condition that allows the forces of weathering to establish a residual soil in which many species soon anchor themselves One of the most efficient of these is *Panicum linearifolium* Scribn Evidence seems to show that it starts almost entirely by seeds from above The warm nature of the talus soil, coupled with its moist condition during the early part of the season, must produce favorable conditions for germination of the many seeds which undoubtedly find lodgment there Probably a very small percentage of the seedlings are able to endure the very dry conditions which obtain during the summer Other species of grass, such as *Danthonia spicata*, *Oryzopsis juncea* and *Oryzopsis asperifolia*, also come in early *Arctostaphylos Uva-ursi* and *Aster macrophyllus* L form mats over the bare fragments, the latter plant is more prominent as conditions become shadier Its large leaves form a very effective mosaic 1–2 dm above the surface and enable more mesic species to start Associated with these in varying proportions are the brake (*Pteris acquilina* L), the salmonberry (*Rubus parviflorus* Nutt) and the bush honeysuckle (*Diervilla Lonicera* Mill), the last plant is often very common on the upper, dryer portions of the slope

The pioneer tree growth consists of small scattered individuals If white birch be the pioneer species, which seems not always to be the case, it is soon followed by the poplar species already mentioned and by scrubby specimens of red oak Besides many seedlings of the species named, several other woody species appear more or less during the early stages of invasion, such as hop hornbeam (*Ostrya virginiana* (Mill) K Koch), arrow-wood (*Viburnum dentatum* L), chokecherry (*Prunus virginiana* L), buffalo-berry (*Shepherdia canadensis* (L) Nutt), *Rubus procumbens* Muhl , *Rosa acicularis* Lindl. and seedlings of basswood, white ash and sugar maple

Early herbaceous species, as such, hardly form a definite stage in the succession in the sense of paving the way for woody growth They may precede or accompany it, but are later controlled by reaction Among the commoner species may be mentioned *Erigeron canadensis* L (horseweed), *Silene antirrhina* L (sleepy catchfly), *Satureja vulgaris* (L) Fritsch (basil), *Aralia hispida* Vent (bristly sarsaparilla), *Convolvulus spithamaeus* L (erect bindweed), *Carex adusta* Boott, *Antennaria neodioica* Greene (everlasting), *Fragaria vesca* L var *americana* Porter (wild strawberry), *Epilobium angustifolium* L (fireweed), *Adlumia fungosa* (Ait) Greene (climbing fumitory), *Apocynum androsaemifolium* L (spreading dogbane) and *Campanula rotundifolia* L (harebell)

The sequence of the invading associations varies greatly at different points along the range While *Betula alba* var *papyrifera* is the dominant pioneer tree species at some points, at others it is *Populus tremuloides* or *Populus grandidentata* The exact ecological relationship between these three species is an interesting problem, but it was not worked out Eventually the invading forest merges with the permanent fringe of forest below the talus The latter is often dominated by sugar maple and red oak, but here again considerable variation occurs, which will be considered later

d) Forest below talus slope

This extends in general from the flood-plain of the valley below to the bottom of the talus slope above, pushing up toward the summit or even reaching it at low points in the range It may vary in width from a mere fringe of trees as at *A*, Figure 8, to several hundred meters at *F* While the tree species are mainly deciduous, especially above, conifers often occur near the bottom These include white and red pine, balsam, arbor vitae, white spruce and hemlock In fact, the last-named species sometimes forms groves of large trees, similar to the climax forest of the north slope

A transect of the forested area was made at a point just east of the saddle in Section 14 Near the top, the talus slope was being rapidly invaded by small oaks and aspens, as shown in Plate XXIII, Figure 1, *Populus grandidentata* being the dominant species, intermingled with scattering white birch and maple saplings A little farther down, the open spaces became fewer and the trees taller (up to 15 m), gradually forming a canopy above and giving perceptibly shadier conditions The soil contained more humus, derived largely from the leaves of the aspens Here patches of *Aster macrophyllus* and *Aralia nudicaulis* formed a large proportion of the ground cover Occasional small specimens of white ash, balsam, hop hornbeam and basswood were noted as invaders at this stage. The unfavorable conditions for anchorage produce remarkable clumping of the stems in certain species, especially in the sapling stage of the hop hornbeam, sugar maple and red oak Nine stems were counted in one specimen of hop hornbeam Basswood overcomes the difficulty by excessive sprouting Approximately half-way down the slope a bench occurred, 15–20 m wide and nearly level A striking feature here was the appearance of rather large conifers, including specimens of white pine (up to 5 dm in diameter), balsam, white spruce and arbor vitae Poplar as the dominant species was replaced by red oak and white birch More mesic conditions were indicated by the presence of such species as *Smilacina racemosa* (L) Desf (false spikenard), *Galium triflorum* Michx (sweet-scented bedstraw), *Hepatica triloba* Chaix (liver-leaf), *Maianthemum canadense* Desf (false lily-of-the-valley), *Streptopus roseus* Michx (twisted-stalk) and *Mitchella repens* L (partridge-berry) Gradually the oaks were replaced by the sugar maple, which became the dominant species to the edge of the flood-plain, with white pine still frequent as a subdominant At the edge of the forest bordering the flood-plain, the increased light and moisture conditions produce a marked change in the ground cover, with a great diversity of species coming in Seedlings of aspen (*Populus tremuloides*) and hazel (*Corylus rostrata*) seem to be responses to the increased light The frequent occurrence of wild black cherry (*Prunus serotina*) along the margin of the forest is undoubtedly a response to the same conditions Groves of aspen saplings mixed with white birch are not uncommon (Pl XXIV) The appearance of many other woody species is due more to the increased moisture along the margin of the flood-plain Among these may be mentioned *Fraxinus nigra* Marsh (black ash), *Salix discolor* Muhl (glaucous willow), *Viburnum Opulus* L var *americanum* (Mill) Aiton (cranberry-tree), *Alnus incana* (L) Moench (speckled alder), *Acer rubrum* L. (red maple), *Spiraea salicifolia* L (meadow-sweet) and *Cornus stolonifera* Michx (red-osier dogwood)

The complex of forest and flood-plain species is extremely variable in its composition. This may be explained partly by the very unstable conditions in the valley and partly by changes in the edaphic conditions produced by gullying down the side of the range, with the consequent deposition of new soil near the bottom of the slope A noteworthy instance of the latter condition occurs opposite the saddle in Section 14 (Pl XXV, Fig 1) Gullying in this case is due to the increased drainage over the saddle, resulting mainly from the melting snow in the spring In the summer its upper portion at least may be dry

2 Hydrarch successions in the valley of Carp River

As before indicated, the mesic forest below the talus slope is bordered by Carp River or its flood-plain This flood-plain is comparatively broad in the vicinity of the lake, owing to the flat nature of the valley At this point the river is a sluggish, meandering stream 20–40 m wide, which does very little vertical cutting, but shifts its course from time to time Carp Lake is merely a broadened part of the river According to Wright (30), the valley resulted not from the erosive action of a former river but from the pounding action of the waves on the shores of a vanished lake which covered the area The present floor of the valley is subject to periodical flooding, in which a certain amount of sediment and débris from higher levels is laid down There is thus a lack of stabilisation in the edaphic conditions which prevents the encroachment of the mesic forest The line of demarcation between forest and flood-plain is usually very abrupt, as shown in Plate XXIV Flooding has the effect of producing irregularities and telescoping in the hydrarch successions paralleling the river, so that these successions are evidently not playing a prominent part in the formation of the forest There are a few points along the range, however, where transitional bog forests may be found One occurs between Sections 13 and 18, T 51 N (Pl XXV, Fig 2) This is near the mouth of a drainage system coming directly from the ridge This forest is quite limited in extent Its interest lies in the suggestion it gives as to the character of the bog forest, which will eventually precede the mesic forest as the latter claims the entire valley The typical tree species are arbor vitae, white spruce, balsam, tamarack and black ash The forest floor is rough and often covered with a mass of shrubs, fallen logs and herbaceous growth. The soil is typical muck of a fine texture In July the water-table was approximately 3 dm below the surface Characteristic herbaceous plants are *Aralia nudicaulis, Aster macrophyllus, Galium asprellum* Michx, *Aspidium cristatum* (L) Sw, *Clintonia borealis* (Ait) Raf, *Circaea alpina* L, *Carex leptalea* Wahlenb and *Habenaria hyperborea* (L) R Br

The hydrarch successions of the river and flood-plain contain many of the elements of typical peat bog areas such as described by Davis (12) for the Upper Peninsula On the other hand, there is a lack of definiteness in the sequence of the associations, and the sphagnum element, with its accompanying vegetation, is not at all common The latter condition is due to the influx of fresh water during at least a portion of the year A year of unusually high flood may destroy the continuity of vegetational development along certain lines This is well attested near the intake of Carp Lake by the dead and dying trunks of small black ash trees Periods of excessive flooding may be measured approximately by the oldest of these After such periods of high water, pioneer species again come in and initiate a new course of succession A patchwork results, which is especially evident in the shrubby vegetation This patchwork is further modified by the varying ability of the different species to withstand the presence of excessive water about their roots The shorter-lived herbaceous forms often show more definite zonation, especially along such restricted areas as mud flats or sandy beaches bordering the river or lake They are able to adapt themselves more readily to changing conditions

In order to illustrate the tendency of the hydrarch successions in the valley, the associations found in the river, lake and flood-plain will be briefly described

a) Carp River (Pl XXVI)

Where this stream flows through the flood-plain it is comparatively shallow with a muddy bottom The slow-moving current makes the ecological conditions very similar to those found along the margins of many of the smaller lakes in the Upper Peninsula Among the immersed aquatics may be mentioned *Potamogeton*

pusillus L , *Potamogeton heterophyllus* Schreb , *Potamogeton zosteriifolius* Schumacher, *Potamogeton amplifolius* Tuckerm , *Potamogeton natans* L , *Myriophyllum Farwellii* Morong, *Ranunculus aquatilis* L var *capillaceus* DC , *Hippuris vulgaris* L

The commonest large aquatic is *Nymphaea advena* Ait (yellow pond lily), it sometimes forms patches extending half-way across the stream *Castalia tuberosa* (Paine) Greene (white water lily) is much less common, though it occasionally occurs in large patches, the same thing may be said of the water shield (*Brasenia Schreberi* Gmel) In many places the stream is fringed with overhanging shrubs, as shown in Plate XXVIII, Figure 1 Mud banks, which often occur at the bends, support various aquatic or amphibious species, such as *Potentilla palustris* (L) Scop (marsh cinquefoil), *Sparganium eurycarpum* Engelm (bur-reed), *Eleocharis acicularis* (L) R & S , *Carex filiformis* Good (bog sedge) and *Carex stricta* Lam The last two species form clumps at various points along the bank and thus enable other species to obtain a footing

The shrubby growth along the banks consists principally of the following *Alnus incana* (L) Moench (hoary alder), *Ilex verticillata* (L) A Gray (winterberry), *Cornus stolonifera* Michx (red-osier dogwood), *Chamaedaphne calyculata* (L) Moench (leather-leaf), *Spiraea salicifolia* Roi (meadow-sweet), *Salix petiolaris* J E Smith, *Salix pedicellaris* Pursh (bog willow) and *Salix lucida* Muhl (shining willow) Two fern species, namely, *Osmunda regalis* L and *Aspidium Thelypteris* (L) Sw , often occur at the margin of the water, more or less shaded by the shrubs *Chamaedaphne calyculata*, though not the commonest shrub lining the river bank, is probably the most important in the formation of floating mats, which often start from sedge hummocks One effect of these floating mats is to cut off quieter bodies of water where various aquatic and amphibious species are more successful in establishing themselves

One thing seems clear in connection with the successions along the margin of the river, namely, their instability Even when Carp Lake, as such, is gone, the river will still continue, though not in its present bed, as the bottom of the valley will have been raised through sedimentation

b) Carp Lake

Carp Lake (Pl II, Fig 1) lies parallel to the main ridges, covering the floor of the valley for a distance of about 2 km Its broadest portion is near the east end (Pl XXVIII, Fig 2), where it has a width of approximately 0 5 km Except at this end, the mesic forest extends nearly to the water's edge At the east end a broad delta has been formed where Carp River enters the lake (Pl XXVII) The submerged part extends well out into the lake, being several hundred meters broad at its widest portion (Pl XXVIII, Fig 2) Here the water is shallow, varying from 3 to 10 dm in depth The west end of the lake is also shallow, and choked with aquatic growth and débris, especially near the outlet In general the beaches are very narrow Most of those on the north side are of the shingle type In places they are entirely lacking and the shore-line is directly bordered by a fringe of shrubs similar to those along the bank of the river Sandy beaches occur on the south side and near the west end on the north side They are broader than the gravel beaches and show more clearly the zonal development of vegetation The edaphic conditions are naturally more stable around the margin of the lake than along the river Especially is this true on the south side where deposition is occurring more rapidly than on the north

The free-floating aquatic vegetation of the lake, being very similar to that of the river, need not be mentioned The best evidences of plant succession are seen on the flat sandy beaches and on muddy flats near the delta At the delta there is a zone of rushes extending from 50 to 100 m out into the lake Its outer part consists of the bulrush (*Scirpus occidentalis* (Wats) Chase), then comes a zone of *Equisetum fluviatile* L (pipes) covering a large area The inner portion of the zone consists of a mixture of *Glyceria borealis* (Nash) Batchelder (northern manna grass), *Leersia oryzoides* (L) Sw (rice cutgrass), and along the muddy shore *Eleocharis palustris* (L) R. & S , *Acorus Calamus* L (sweet flag), *Dulichium arundinaceum* (L) Britton, *Polygonum amphibium* L (water smartweed), *Glyceria canadensis* (Michx) Trin (rattlesnake grass), *Scirpus atrovirens* Muhl , *Eleocharis obtusa* (Willd) Schultes (blunt spike-rush) and *Sagittaria latifolia* L forma *gracilis* (Pursh) Robinson, apparently the common form in northern Michigan The immediate shore is fringed with clumps of *Salix lucida*, interspersed with open areas covered with *Calamagrostis canadensis* (Michx) Beauv (bluejoint) Logs lying almost concealed tell the story of flooding at this point, this is also shown by standing specimens of *Alnus incana* and *Salix petiolaris*, dead above, but making vigorous new growths at the base

In the shallow water bordering the sandy beaches the rushes are often accompanied by areas of pipewort (*Eriocaulon articulatum* (Huds) Morong) This may produce unusually long stems when growing with *Scirpus occidentalis* Among the commoner species occurring on the sandy beaches are the following *Juncus brevicaudatus* (Engelm) Fernald, *Hypericum ellipticum* Hook (pale St John's-wort), *Cladium mariscoides* Torr (twig-rush), *Ranunculus Flammula* L (smaller spearwort), *Mimulus ringens* L (monkey flower), *Sium cicutaefolium* Schrank (water parsnip), *Agrostis hyemalis* (Walt) BSP (hair grass), *Carex crinita* Lam , *Carex rostrata* Stokes and *Carex Oederi* Retz Both the sandy and gravelly beaches are very often backed by a shrubby association composed of *Chamaedaphne calyculata*, *Ilex verticillata* and *Alnus incana* With these often occur *Spiraea salicifolia* and *Fraxinus nigra*, which fringe the mesic forest

It is evident from the foregoing description that the transition from lake to mesic forest is rather abrupt, this is especially true on the north side of the lake, where the angle of slope is greatest The few associations noted along the narrow beaches consist of plants which are able to endure submergence for brief periods The shrubby growth backing the beaches, though only a little above the mean level of the lake, is high enough to escape most of the destructive influences of high water

c) Flood-plain

On account of the varying influences to which the flood-plain is subjected, the successions are not, in general, well marked In the broader portions of the valley, as in Section 24, T 51 N , R 43 W , there is a dense growth of *Alnus incana*, intermingled with occasional individuals of tamarack. In the northwest corner of this section there is a small "tamarack swamp" forming a typical stage in the filling up of a peat bog. The ecological stages of such a bog have been well described by Transeau (27), Cooper (6) and others and will not be treated here. In Sections 23 and 14, immediately east of the lake, the flood-plain is covered by a grassy marsh (Pl. XXIV), with a shrubby zone lining the river, as already described. The flora of this area is very composite in character. Portions of it are dominated by a dense growth of bluejoint (*Calamagrostis canadensis*). The species observed here include the following: *Asclepias incarnata* L., *Verbena hastata* L., *Aster puniceus* L., *Eupatorium purpureum* L., *Scirpus Cyperinus* (L.) Kunth, *Osmunda regalis* L., *Onoclea sensibilis* L., *Solidago serotina* Ait., *Anemone canadensis* L., *Chelone glabra* L., *Aspidium Thelypteris* (L.) Sw., *Pteris aquilina* L., *Glyceria canadensis* (Michx.) Trin., *Lysimachia terrestris* (L.) BSP., *Iris versicolor* L., *Cicuta bulbifera* L., *Scutellaria lateriflora* L., *Thalictrum dasycarpum* Fisch. & Lall., *Galium asprellum* Michx., *Geum strictum* Ait., *Impatiens biflora* Walt., *Rumex verticillatus* L., *Hypericum virginicum* L., *Campanula uliginosa* Rydb., *Phalaris arundinacea* L., *Clematis virginiana* L., *Leersia oryzoides* (L.) Sw., *Humulus Lupulus* L., *Ranunculus pennsylvanicus* L. f., *Galium Claytoni* Michx., *Radicula palustris* (L.) Moench, *Carex filiformis* L. and *Carex tribuloides* Wahlenb.

The grassy marsh described above undoubtedly occupies the position of a former delta. It thus represents a stage in the gradual filling up of the valley with sediment and organic remains.

SUMMARY

The ranges of the Porcupine Mountains are entirely surrounded by a low plain, so that the mountains were islands for some time after the final retreat of the ice-sheet. As the water subsided, the higher ranges to the south were first uncovered. Pioneer invasion probably took place where the wash of the waves was not too severe, following stages analogous to those found in the present shore-line. At the present time, these southern ranges or hills, including Government Peak, the highest point, are clothed with a mesic forest to the very top (Pl II, Fig 1) This forest was possibly preceded by a xeric coniferous forest dominated by pine species, as suggested by Ruthven (1, p 27) In this case the pines began their invasion near the water's edge and followed the heath-mat stage They made their last stand at the top of the mountains, being followed up and replaced by a mesic forest, whose successions are correlated with the greater accumulation of soil near the base of the slope

The top of the first range is unique in still holding out against the mesic forest This is undoubtedly due to the peculiar topography of this range As is evident from Figure 2, this topography is associated with the presence of Carp Lake, which once covered a much greater area than at present The dip of the strata toward the north, coupled with the subsidence of Carp Lake, has created a great cliff or escarpment, which is continually wearing away and producing a talus slope at its foot

The development of vegetation over the region has led to two climax formations, namely, the hemlock climax and the maple climax

The presence of the hemlock climax on the north slope of the first range seems to be conditioned by the physical factors of temperature, moisture and light Greater humidity and more uniformity in temperature near the shore are due to the presence of a large body of water The average temperature of points along the coast is several degrees warmer than inland locations a few miles back, and the average precipitation during the winter months is 30 per cent more than at Bergland, 26 km back from the shore Reduced light intensity at the lower, more humid, elevations on the north slope is probably more favorable to hemlock as compared with maple

The maple climax occurs on the higher portions of the first range (except the summit) and on the ranges farther south As compared with hemlock, maple seems to be more tolerant of extremes of temperature and light

The principal succession leading to the hemlock climax is along the shore The pioneers in the more exposed situations are crevice plants In the severer situations these can initiate only very short or incomplete lines of succession Where conditions are less severe, which may be only a few meters farther inshore, the pioneers consist of lichens, mosses and crevice plants, which lead to more definite lines of advance, but the irregularities of the shore-line produce such varied conditions that there is often a lack of any gradual transition from lower to higher ecological forms At practically all points along the shore the climax forest has pushed down to the limit of its possible extension under present conditions, and this has resulted in a telescoping of the ordinary transitional stages

Lines of succession leading to the maple climax may be seen at the summit of the first range and in the valley of Carp River In the first case the climax is reached through xerarch series, beginning with crustose lichens and xeric mosses on the exposed rock surface of the summit One of the principal pioneers is *Selaginella rupestris*, which often forms a layer of humus 1–2 dm thick This, together with various low-growing species, including crevice plants such as *Danthonia spicata* and *Panicum depauperatum*, paves the way for the heath mat, which is composed largely of two species of Vaccinium (see p 43) A zone of scrubby conifers and oaks then leads gradually to the maple climax on the north side of the summit

On the south side the presence of the cliff forms a direct barrier to invasion from below, except where the escarpment has been worn down so as to produce a saddle across the range Below the escarpment there is a talus slope of varying width, fringed by a mesic forest that extends below to the flood-plain of Carp River In general, this mesic forest is young and heterogeneous in character, but it is approaching the maple climax Its upper border is irregular, but forms a more or less sinuous curve representing a line of invasion on the talus Since the width of the talus depends on the height of the escarpment, the line of invasion extends high at low points in the range

Successional continuity on the talus is more or less broken, at least in the earlier stages Lichens and certain moss species are undoubtedly important, but *Betula alba* var *papyrifera* is one of the noteworthy pioneers adapting itself to unusually severe conditions This is followed sooner or later by aspens, after which there is a gradual transition toward the mesic climax

As the cliff wears down, the summit of the range will eventually be claimed by the mesic forest At present the xerarch series forms a connecting link between the maple climax in the valley and that on the north side of the summit

The lower edge of the mesic forest below the talus forms an abrupt border to the flood-plain of Carp River This is due to periodical flooding, which produces irregularities and telescoping throughout the hydrarch series on the comparatively flat floor of the valley Any marked building up of the mesic climax from this source must, therefore, await a change in physiographic conditions along the river valley This will come with the gradual filling up of the valley through sedimentation, thus changing the conditions under which flooding now occurs The present successions along the valley of Carp River and Carp Lake are of comparatively little moment, they indicate, however, the character of a

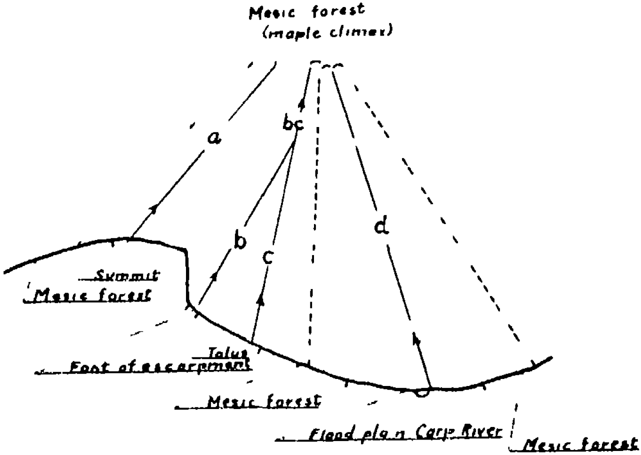


FIG 11 Diagram showing lines of vegetational development leading to the maple climax on the first range

portion of the hydrarch series which will eventually lead to a mesic climax covering the entire floor of the valley

The principal zones of vegetation in connection with the development of the maple climax on the first range are shown in the diagram (Fig 11) The *letters a, b, c, d* indicate the lines of succession The line *a* begins with lichens, mosses and crevice plants at the bare summit and culminates in the maple forest on the north slope, *b* originates largely from seeds washing over the summit, *c* represents a line of invasion on the talus slope from the forest below, *d* is a broken line representing the discontinuous nature of the hydrarch succession from the valley of Carp River Part of this succession leads to the mesic forest on the second range

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PLATE II

Fig 1 Carp Lake from top of first range, looking southwest, second and third ranges in distance, escarpment of first range extending west-southwest (extreme right), outlet of lake at far end, Government Peak (highest point in the Porcupine ranges) in distance to left

Fig 2 Exterior view of hemlock climax along a "forty" line where the timber has been cut, elevation about 100 meters above Lake Superior, two sugar maples at right large hemlock in background, salmonberry and three small hemlocks in foreground (see text, p 19)

PLATE II

FIG. 1

FIG. 2

PLATE III

A view showing distribution of yellow birch and sugar maple with conifers *removed; looking northeast toward Lake Superior; edge of forest to left;* trees in foreground mostly maples. Note abundant growth of salmon berry as a ground cover (see text, p. 19).

PLATE III

PLATE IV

Interior view of mesic forest about one kilometer from shore of Lake Superior (Section 16, T. 51 N., R. 42 W.); hemlock dominant tree at this point on slope; a large yellow birch in foreground at left; portion of crown of sugar maple in background at right. Note gentle slope (toward Lake Superior) (see text, p. 19).

PLATE IV

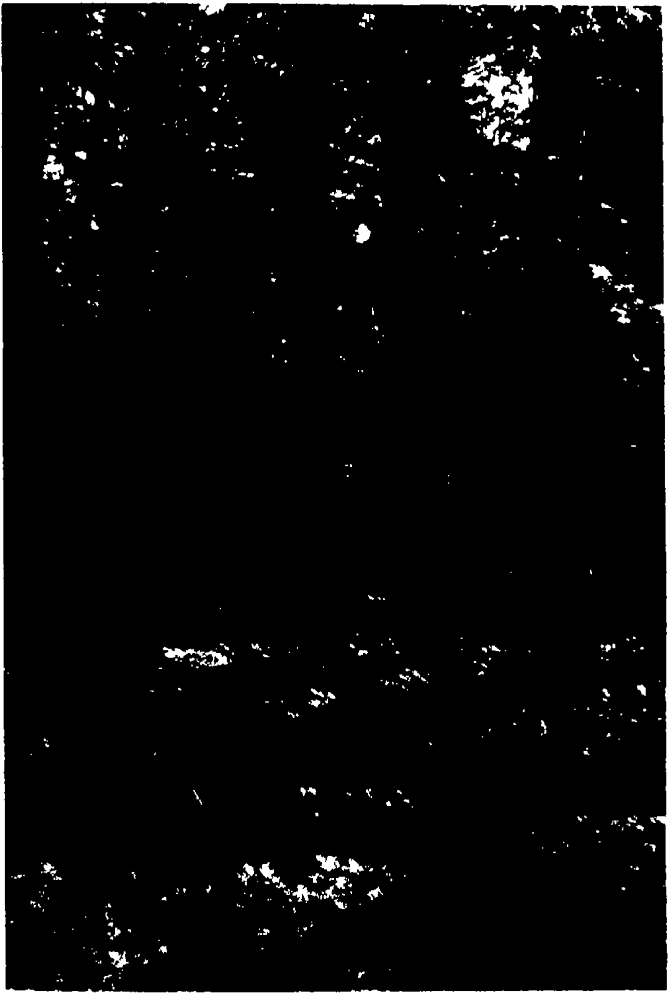

PLATE V

A wetter more open portion of the forest in which the dominant large tree is arbor vitae, in foreground salmonberry and seedlings of maple balsam and white spruce Other tree seedlings observed were yellow birch basswood and white ash (see text p 19)

PLATE V

PLATE VI

Stand of sugar maple approximately 100 meters north of summit of ridge in Section 14, T. 51 N., R. 43 W.; maple seedlings in foreground; trees here somewhat larger than typical. Note comparatively clear forest floor (see text, p. 21).

P

PLATE VII

FIG. 1. Seedlings of sugar maple in hemlock forest; those shown 1.5–3.0 decimeters high, approximately 40 individuals per square meter (see text, p. 21).

FIG. 2. View along an old wood road, which here acts as an artificial windfall; dense growth of young maples (2–6 meters high) on each side of road; salmonberry in foreground.

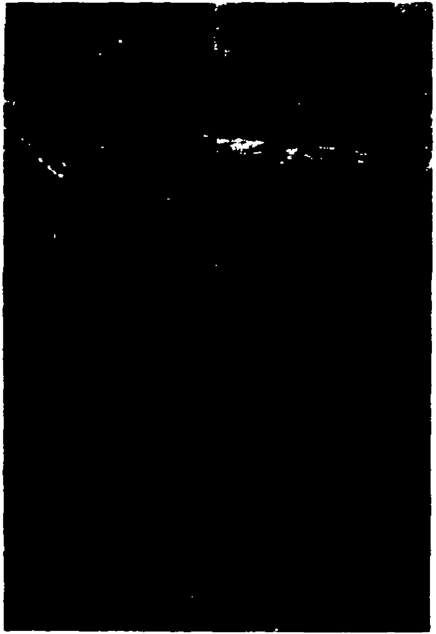

FIG 2

PLATE VIII

FIG. 1. Rocky shore a few miles west of Union Bay, showing sandstone beds dipping toward north; edges of the tilted strata offshore forming a rocky terrace which breaks more or less the force of the waves. Vegetation readily establishes itself in the joint and bedding planes as shown. The white coating on the rock surface is *Parmelia lactea* (see text, pp. 31, 32).

FIG. 2. Narrow shingle beach in which the forest comes unusually close to the water's edge, being protected from the winter storms by the ledge of rock offshore. Note zone of white birch and arbor vitae lining the shore at this point, bordered by salmonberry and *Cornus alternifolia*. *Equisetum arvense* is growing in the shingle (see text, p. 31).

FIG 1

FIG 2

PLATE IX

Deschampsia caespitosa and *Aster Faxoni* growing in a typical situation along the shore. Note dip of the strata and fragmental character of the rock (see text, pp. 32–33).

PL

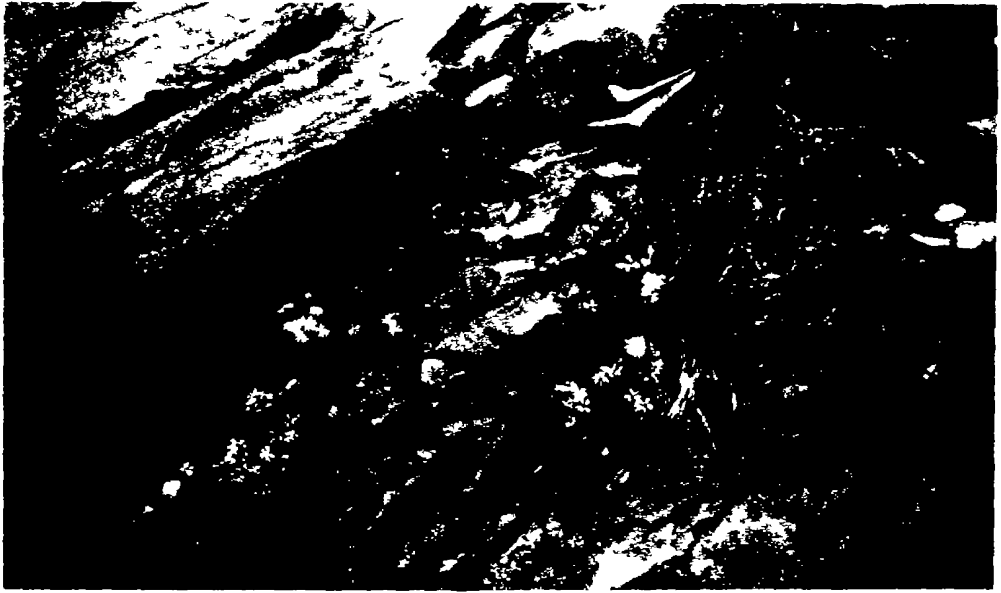

PLATE X

Rock surface well above the wash of the waves patches of crustose lichen in foreground *Stereocaulon paschale* large white patches *Parmelia lactea* low dark patches *Grimmia apocarpa* *Polypodium vulgare* in crevices near top of boulder (see text p 43)

TE

PLATE XI

A wall of conglomerate paralleling the shore and forming a protective barrier to the forest behind it, conifers and aspens growing under xeric conditions at the top The conifers include a small white pine (in the background) small specimens of white spruce balsam and arbor vitae all growing in the crevices of the rock

TE

PLATE XII

Showing the roots of white pine running for several meters along the surface and finally acting as an agent of rock displacement. Small red pine and aspens border the shore in the background. The roots on the far side of the tree are covered by a mat of *Arctostaphylos Uva ursi* (see text, p. 34).

TE

PLATE XIII

Fig. 1. Broad type of shingle beach, devoid of vegetation on account of the wash of the winter waves.

Fig. 2. North slope of first range looking west, showing a ‘burn’ in the hemlock forest three years after the fire. Note angular character of sandstone fragments underlying forest floor, the humus being completely destroyed (see text, p. 35).

PLATE XIII

PLATE XIV

FIG. 1. Cliff and talus slope, first range; view from a point just east of Carp Lake, looking north. Top of cliff at this point is about 130 meters above floor of the valley of Carp River and 240 meters above Lake Superior, the face of the escarpment here being approximately 65 meters high. Note fringe of forest between talus slope and river valley (see text, p. 38).

FIG. 2. View of cliff in Section 15, T. 51 N., R. 43 W., looking east. In foreground are shown last stages of the cliff preceding formation of a saddle. Soil has accumulated on the bare rock in places. Note xeric character of the vegetation (see text, pp. 38, 39).

PLATE XIV

FIG. 2

PLATE XV

Limit of forest growth on summit of ridge looking east clump of small red pines in background (to left) bearberry mat on rock in foreground The prevailing wind is from the southwest which is more or less evident from the general direction of the branches in the small pines shown (see text pp 11 12)

PLATE X

PLATE XVI

Portion of the summit looking east, Carp River in valley below (at right) small red pines and stunted aspens at left back of which a transition zone occurs as shown in Plate XVIII leading to the maple climax of the north slope Note pines growing from crevices in face of escarpment

PL

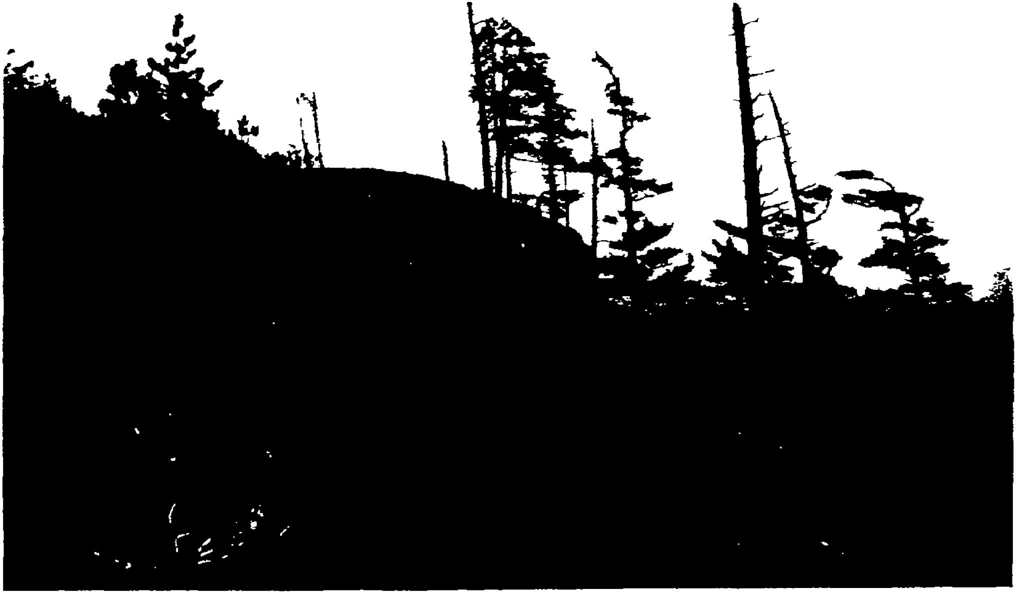

PLATE XVII

Close up view of rock surface, crest of ridge; plants in foreground, *Juniperus communis* var. *depressa*, *Danthonia spicata*, *Antennaria neodioica*, *Potentilla tridentata*, *Polygonum Douglasii* (lower right), *Solidago randii* var. *monticola* in the background, and *Parmelia conspersa*, the dominant lichen (on rock surfaces) (see text, pp. 41-42).

PL

PLATE XVIII

Zone of transitional tree growth at quadrat 5 (Fig. 10) showing bare rock surface in places and *Danthonia spicata* as the conspicuous grass species. Note red pines (at right) and aspens and small red oaks (at left) (see text p. 45)

PLATE X

PLATE XIX

Overhanging ledge of cliff shown in Figure 8 F illustrating dip of the strata (sandstone) Various plants gain a foothold in the moist crevices (see text p 48) Picture taken from underneath the ledge looking up

PLATE XIX

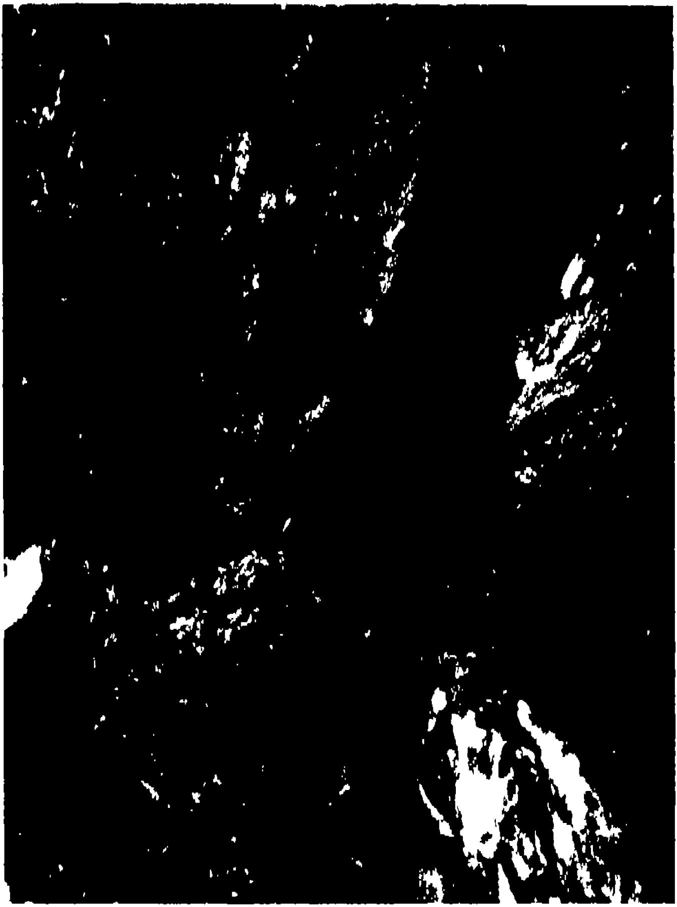

PLATE XX

Rock ledge on face of escarpment, looking east. In foreground, two small white pines and small specimens of *Prunus pennsylvanica*, *Rhus typhina* and *Cornus circinata*; also *Arctostaphylos Uva-ursi*, *Artemisia caudata* and *Danthonia spicata*, *Woodsia ilvensis* and *Campanula rotundifolia* growing from rock crevices; in background, small red pine and leaves of oak (*Quercus rubra*) showing below. *Parmelia conspersa* on rock surface above and below.

PLATE XX

PLATE XXI

FIG. 1. View of first range looking east in Section 14, valley of Carp River (at right). Shows stage in reduction of escarpment and advance of forest up the slope (see text, p. 49).

FIG. 2. Bottom of talus slope immediately west of saddle in Section 14, looking east, showing characteristic clumping habit of white birch when growing in talus; angle of slope here about 30 degrees. The cliff at this point is very high and the talus field 200 meters or more in width (top to bottom). Note line of forest as it creeps over saddle across low point of range (see text, pp. 49-50).

PLATE XXI

FIG. 1

FIG. 2

PLATE XXII

Lichens and mosses on talus slope (see Pl. XXI). *Parmelia conspersa* (the most conspicuous foliose lichen); three species of *Cladonia* (lower right), *C. rangiferina*, *C. sylvatica* and *C. pyxidata*; *Hedwigia albicans* (extreme left) (see text, p. 50).

[redacted]

[redacted]

PLATE XXIII

Fig 1 An advanced stage in the invasion of the talus slope showing pioneer tree species consisting of *Populus grandidentata* and small specimens of *Quercus rubra* and *Pinus Strobus* Note small size of rock fragments (sandstone)

Fig 2 View of escarpment looking north vertical rock face about 70 meters high at this point below this 200–300 meters of talus material being invaded by pines and aspens Below the talus slope is the front of the advancing forest which slopes to the valley of Carp River below

PLATE XXIII

FIG. 2

PLATE XXIV

Lower edge of forest bordering flood plain in the background *Betula alba* var *papyrifera* *Populus tremuloides* *Acer rubrum* *Cornus stolonifera* *Salix rostrata* and *Salix petiolaris* large tree in foreground is black ash (*Fraxinus nigra*)

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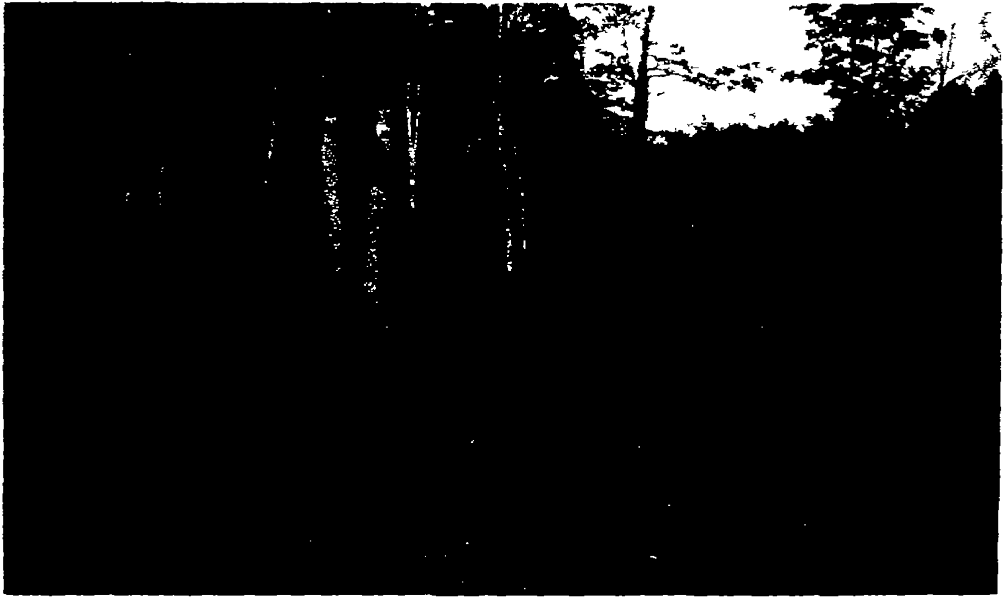

PLATE XXV

FIG. 1. Gullying on south side of first range, about half way down the slope; white birch and aspen in background; in foreground small specimens of sugar maple and yellow birch; shows clumping specimens of hop hornbeam (*Ostrya virginiana* upper right); ground cover mainly composed of *Aralia nudicaulis* (see text, p. 54).

FIG. 2. Cedar swamp, north edge of Carp River Valley, showing large specimens of arbor vitae (*Thuja occidentalis*) near center of figure; in background *Alnus incana* and *Cornus stolonifera* (see text, pp. 54, 55).

FIG 2

PLATE XXVI

Carp River from summit of first range looking east southeast flood plain in the distance covered by alder swamp The river flows west emptying into Carp Lake (see text p 55)

PLATE XXVI

PLATE XXVII

Delta east end of Carp Lake Looking east showing narrow channel of Carp River in background first range in the distance showing saddle in Section 14 in foreground *Scirpus occidentalis* *Equisetum fluviatile* and *Nymphaea advena* (see text pp 57 58)

PLATE XXVIII

FIG. 1. Carp River near north edge of flood plain; top of first range just visible in background (at upper right). *Alnus incana* lining bank at this point. Aquatics are *Nymphaea advena* and *Sparganium eurycarpum* (water's edge right and left).

FIG. 2. East end of Carp Lake, looking south toward second range. The zone of rushes (*Scirpus occidentalis*) marks the shallow water over the submerged portion of the delta. The group of balsams along opposite shore indicates the presence of a small stream flowing into the lake.

Fig 1

Fig 2

ADDITIONS TO AN ANNOTATED LIST OF THE HIGHER PLANTS OF THE REGION OF DOUGLAS LAKE, MICHIGAN II *

FRANK C GATES

Kansas State Agricultural College

AND

JOHN H EHLERS

University of Michigan

THE collections and records of the summers of 1927, 1928 and 1929 are the material upon which this second list of additions is based During these summers improved transportation facilities at the Biological Station have given the authors a better opportunity to make a more thorough survey of the less accessible parts of Emmet and Cheboygan counties

These records are made in the same general form employed in the authors' previous publications [1] on the species of higher plants in the region about Douglas Lake, comprising Emmet and Cheboygan counties A revised summary of species by region and counties follows the list This paper completes the authors' statement of the flora of the region for the time (1909–29) during which the Biological Station occupied the original site

Although parts of the two counties which are not readily accessible from the Station still remain unexplored, the list of the summer flora is now fairly complete A thorough survey of the

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* Contribution 308 from the Department of Botany and Plant Pathology Kansas State Agricultural College, and Paper 336 from the Department of Botany of the University of Michigan

[1] Gates, Frank C, and Ehlers, J H "An Annotated List of the Higher Plants of the Region of Douglas Lake, Michigan," *Pap Mich Acad Sci, Arts and Letters*, 4 183–284, 1924 "Additions to an Annotated List of the Higher Plants of the Region of Douglas Lake, Michigan" *ibid*, 8 111–121, 1927

region during early spring and late fall would doubtless extend the list somewhat This the authors have not been able to accomplish

PLANTS FOUND IN THE REGION FOR THE FIRST TIME SINCE THE PREPARATION OF THE PREVIOUS LISTS OR OF WHICH THE IDENTIFICATION HAS BEEN MADE SUBSEQUENTLY TO THE PUBLICATION OF THOSE LISTS

(At the extreme right C = Cheboygan County and E = Emmet County)

Phylum PTERIDOPHYTA

11 POLYPODIACEAE (Fern Family)

DRYOPTERIS ROBERTIANA (Hoffm) C Chr (*Phegopteris Robertiana* (Hoffm) A Br) C
East part of Reese's Bog, 1927 (C D La Rue)

Phylum CALAMOPHYTA

2 EQUISETACEAE (Horsetail Family)

EQUISETUM KANSANUM SCHAFFNER E
Railroad ballast, Little Traverse Bay, 1925

EQUISETUM PRAEALTUM Raf C
Michigan Central Railroad near Mullet Lake, 1925

Phylum LEPIDOPHYTA

1 LYCOPODIACEAE (Club-Moss Family)

LYCOPODIUM COMPLANATUM L
Near Reese's clearing, 1927 (G E Nichols), ridge between south tower and Camp Davis, 1929

Phylum ANTHOPHYTA

9 POTAMOGETONACEAE (Pondweed Family)

POTAMOGETON INTERIOR Rydb C
In Nigger Creek, 1928

10 LILIACEAE (Lily Family)

ALLIUM SCHOENOPRASUM L C
Cultivated in Riggsville, 1927

24. ARACEAE

SPIRODELA POLYRHIZA (L.) Schleid. C
A floating aquatic in the Maple River delta, 1928.

30. CYPERACEAE (Sedge Family)

ELEOCHARIS ROSTELLATA Torr. E
Marshy margin of Wycamp Lake, 1929.

CAREX CHORDORRHIZA Ehrh. C
Mud Lake Bog, 1929 (L. S. Ehlers).

CAREX AQUATILIS ELATIOR Bab. F
Wet ground along the Grand Rapids and Indiana Railroad north of Carp Lake, 1928.

31. POACEAE (Grass Family)

BROMUS HORDEACEUS L. C
In a cottage yard, north shore of Burt Lake, 1927.

BROMUS HORDEACEUS GLABRESCENS (Coss.) Shear C
In a cottage yard, north shore of Burt Lake, 1927.

BROMUS JAPONICUS Thunb. C
Winter annual grass planted at the Biological Station in 1927. Two years later many more individuals, but these smaller in size.

ERAGROSTIS FRANKII Steud. F
A weed in the mill yard at Pellston, 1928.

LOLIUM PERENNE L. C
In a cottage yard at the north shore of Burt Lake, 1927.

LOLIUM MULTIFLORUM Lam. C
In the cottage yard at the north end of Burt Lake, 1927.

KOELERIA CRISTATA (L.) Pers. C
Grass transplanted to the Biological Station Grounds from Sleeping Bear Dune in 1927, 1928.

PANICUM BOSCII Poir. C
In beech-maple forest on Colonial Point, 1929 (W. E. Steidtmann).

PANICUM BOREALE Nash L
Wet woods bordering Wycamp Lake, 1929.

60 RANUNCULACEAE (Crowfoot Family)

ANEMONE QUINQUEFOLIA L. E

Herb in aspen woods west of Maple River northeast of Pellston (A. Sharp)

RANUNCULUS REPENS L. C

Roadside ditch north of Topinabee, 1927

RANUNCULUS ACRIS, double-flowered C

Ruderal southwest of Cheboygan. Presumably an escape, but spreading, 1929

85 OXALIDACEAE (Wood Sorrel Family)

OXALIS CORNICULATA L. E

In a field near Bay View, 1923

118 VIOLACEAE (Violet Family)

VIOLA PEDATA L. C

Two plants set out at the Biological Station in 1926, from Grayling. One blossomed in June, 1929

VIOLA HIRSUTULA Brainerd C

In rotting wood in the second-growth beech-maple forest at Riggsville Corners, 1929

VIOLA NEPHROPHYLLA Greene F

In coniferous woods at Cecil, 1928 (G. F. Nichols)

VIOLA ARVENSIS Murray C

In a timothy field, south of Riggsville, 1929

126 PAPAVERACEAE

PAPAVER RHOEAS L. (Corn Poppy) F

Roadside herb, McGulpin Point, 1929

CAPNOIDES AUREUM (Willd.) Kuntze (*Corydalis aurea* Willd.) E

Ruderal in gravel in Big Stone Bay, 1928

132 BRASSICACEAE (Mustard Family)

NEOBECKIA AQUATICA (Eaton) Britton (*Radicula aquatica* (Eaton) Robinson) C

An aquatic herb in Nigger Creek. Locally abundant in this one station in the region, 1927 (G. R. La Rue)

Hesperis matronalis L. Dame's Rocket C
Banks of Cheboygan River, Cheboygan, 1929

Barbarea barbarea (L.) MacM. (*Barbarea vulgaris* R. Br.) F
On shore at Big Stone Bay, 1923

133. CARYOPHYLLACEAE (Pink Family)

Alsine graminea (L.) Britton (*Stellaria graminea* L.) E C
Ruderal (U. S. Highway 23) near Topinabee, 1927, and in the Larix-Thuja association at Round Lake, 1923

Vaccaria Vaccaria (L.) Britton (*Saponaria Vaccaria* L.) C
Weed in the experimental bird pens, 1928 (Helen R. Coburn and Doris Dean)

140. SALICACEAE (Willow Family)

Salix amygdaloides Anders. C
Tree in roadside ditch west of Cheboygan, 1929

Salix candida × **S. discolor** F
A hybrid shrub at Cecil, 1927

Salix candida × **pedicellaris** C
Hybrid willow at Blanchard Lake, 1929. Leaves with the texture and color of *S. candida*, but the length of *S. pedicellaris*.

147. POLYGONACEAE (Buckwheat Family)

Rumex Patientia L. C
Weed near Bryant's Hotel, 1928 (Helen R. Coburn and Doris Dean)

Polygonum tomentosum Schrank C
Weed along the shore of Fairy Island, 1928 (Helen R. Coburn and Doris Dean)

148. NYCTAGINACEAE (Four-o'clock Family)

Allionia nyctaginea Michx. (*Oxybaphus nyctagineus* (Michx.) Sweet) C
Weed in Ballast of Michigan Central Railroad, Mackinaw City, 1929

152 Plantaginaceae (Plantain Family)

Plantago Purshii R & S
Weed in timothy field near Riggsville, 1929
Plantago aristata Michx
Ruderal near Mud Lake, 1929

169 Boraginaceae (Borage Family)

Cynoglossum boreale Fernald C
Beech-maple forest on Colonial Point, 1929

171 Solanaceae (Nightshade or Potato Family)

Lycium halimifolium Mill C
Near an abandoned cabin on the Topinabee Road, 1929

172 Oleaceae

Fraxinus lanceolata Sarg (Included in *F pennsylvanica* in B & B) C
A tree on the ice-ridge at the base of Colonial Point near Maple River delta, 1928 Also north shore of Burt Lake

176 Apocynaceae (Dogbane Family)

Vinca minor L C
On a roadside stone pile near Riggsville, 1929

178 Scrophulariaceae (Figwort Family)

Pentstemon Pentstemon (L) Britton (*P laevigatus* Aiton)
A single plant in a timothy field near Mud Lake, 1929
Veronica officinalis L E
Dry sandy soil in mixed coniferous and beech-maple woods near Harbor Springs and in a similar situation south of Cross Village

191 Lamiaceae (Labiatae) (Mint Family)

Salvia nemorosa Crantz E C
Shrubby herb along a fence-row northeast of Larks Lake and in a yard at Munro Lake, 1929

192 ROSACEAE (Rose Family)

ROSA MICHIGANENSIS Eileen W Erlanson C
East end of the Biological Station along Douglas Lake, 1928 (Eileen W Erlanson)

ROSA SCHUETTEANA E W Erlanson C
The rose heretofore known in the region as *Rosa carolina* is probably this Douglas Lake, 1919 (Mrs Deam), 1924 (Eileen W Erlanson)

ROSA SUFFULTA Greene F C
Along road west of Carp Lake and in the jack-pine plains near Black River, 1927

194 PRUNACEAE (Peach Family)

PRUNUS ALLEGHANIENSIS Porter var DAVISII Wight C
Jack-pine plains south of Burt Lake, 1929

199 FABACEAE (Pea Family)

VICIA AMERICANA Muhl C
Ruderal along U S Highway 27 at Topinabee, 1929

VICIA HIRSUTA (L) Koch C
In the aspens just south of Camp Davis, 1929

VICIA ANGUSTIFOLIA L C
Along the west (1927) and north (1929) shores of Burt Lake

LATHYRUS OCHROLEUCUS Hook C
Ruderal, U S Highway 27 at Topinabee, 1929

224 HALORAGIDACEAE (Water Milfoil Family)

MYRIOPHYLLUM VERTICILLATUM PECTINATUM Wallr C
Nigger Creek, 1927

271 FAGACEAE (Beech Family)

CASTANEA DENTATA (Marsh) Borkh E
Tree, planted in an abandoned orchard southwest of Brutus, 1929

276 APIACEAE (AMMIACEAE or UMBELLIFERAE)

(Carrot Family)

CARUM CARUI L Caraway C
Roadside herb west of Cheboygan, 1929

279 CAPRIFOLIACEAE

SYMPHORICARPOS RACEMOSUS Michx C
Shrub in the jack-pine plains east of Indian River, 1927

SOLIDAGO SP (nearest to *S Houghtonii* T & G) C
Shore of Lake Huron at Pries' Landing, 1929

ASTER LINDLEYANUS T & G C
Shore of Lake Huron at Pries' Landing and Reese's Bog, 1929

ASTER *SAGITTIFOLIUS* Wedemeyer C
Roadside north of Cheboygan

298 CARDUACEAE

CENTAUREA NIGRA L C
Herb, on refuse dump, Indian River, 1928 (C L Kennedy)

CENTAUREA MACULOSA Lam C
Ruderal along the Green Star Trail in Inverness township, 1927

300 LACTUCACEAE

TARAXACUM ERYTHROSPERMUM Andrz E
A single plant in the recently cut-over beech-maple forest west of Pellston, 1928

SONCHUS OLERACEUS L C
Weed in waste places, Cheboygan, 1929

Since the publication of the previous lists, the species listed below have been found in the second of the two counties of the region and are now recorded from both Emmet and Cheboygan counties, Michigan.

The following entries add Emmet County to the published list

Phylum ANTHOPHYTA

1 ALISMATACEAE (Water Plantain Family)

ALISMA SUBCORDATUM Raf E C
In ditch near Carp Creek near Carp Lake, 1928

18 JUNCACEAE (Rush Family)

JUNCUS CANADENSIS J Gay E C
In bog along Grand Rapids and Indiana Railroad north of Carp Lake, 1928

30 CYPERACEAE (Sedge Family)

CAREX CRYPTOLEPIS Mackenzie E C
Wet woods along Wycamp Lake, 1929

31 POACEAE (Grass Family)

BROMUS KALMII A Gray E C
In Big Stone Bay

SPHENOPHOLIS PALLENS (Spreng) Scribn E C
Stony shore, Big Stone Bay and Little Traverse Bay

PANICUM TENNESSEENSE Ashe F C
In the aspens west of Maple River northeast of Pellston and along Little Traverse Bay

45 ORCHIDACEAE (Orchid Family)

CYPRIPEDIUM ARIETINUM R Br E C
Low dunes and interdunal areas under pine in Big Stone Bay

COELOGLOSSUM BRACTEATUM (Willd) Parl (*Habenaria bracteata* (Willd) R Br) E C
Coniferous woods near Cross Village, 1924

132 BRASSICACEAE (Mustard Family)

RADICULA PALUSTRIS (L) Moench E C
Along west Maple River in the mill yard at Pellston, 1928

SOPHIA INCISA (Engelm) Greene (*Sisymbrium incisum* Engelm) E C
Ballast of Grand Rapids and Indiana Railroad north of Carp Lake, 1928

ARABIS DRUMMONDI A Gray E C
Dunes south of Sturgeon Bay, 1929

193 MALACEAE (Apple Family)

AMELANCHIER SANGUINEA DC (*A spicata*, but not *A sanguinea*, of former list) E C
Shrub on sand dunes in Sturgeon Bay, 1929

AMELANCHIER HUMILIS Wiegand E C
Low shrub on sand dunes in Sturgeon Bay, 1929

194 PRUNACEAE (Peach Family)

PRUNUS CUNEATA Raf E C
A low shrub in the aspens west of Maple River east of Pellston, 1928

199 FABACEAE (Pea Family)

TRIFOLIUM AGRARIUM L E C
Ruderal along U S Highway 31 near Mackinaw City and also south of Pellston, spreading

VICIA VILLOSA Roth E C
Fields east of Pellston

238 CELASTRACEAE (Staff-Tree Family)

CELASTRUS SCANDENS L Climbing Bittersweet E C
Liana on wooded sand dunes in Sturgeon Bay, 1929

278 RUBIACEAE (Madder Family)

GALIUM LABRADORICUM Wiegand E C
Cleared Thuja swamp, Grand Rapids and Indiana Railroad, Little Traverse Bay

281 VALERIANACEAE (Valerian Family)

VALERIANA OFFICINALIS L Garden Valerian E C
Herb in roadside ditch south of Carp Lake, 1929

293 ASTERACEAE

ASTER HIRSUTICAULIS Lindl E C
In low open wet area near W Maple River west of Pellston, 1929

The following species add Cheboygan County to our lists

Phylum STROBILOPHYTA

PINACEAE (Pine Family)

JUNIPERUS HORIZONTALIS Moench E C
Pries' Landing, Lake Huron, 1929

Phylum ANTHOPHYTA

4 SCHEUCHZERIACEAE (Arrow grass Family)

TRIGLOCHIN PALUSTRIS L E C
Pries' Landing, Lake Huron, 1929

10 LILIACEAE (Lily Family)

TRIANTHA GLUTINOSA (Michx) Baker (*Tofieldia glutinosa* (Michx) Pers) E C
Pries' Landing, shore of Lake Huron, 1929

ERYTHRONIUM AMERICANUM Ker E C
Beech-maple woods, Colonial Point and second-growth hardwoods at Riggsville Corners, 1926

30 CYPERACEAE (Sedge Family)

RYNCHOSPORA CAPILLACEA Torr var LEVISETA E J Hill E C
Pries' Landing, Lake Huron, 1929

CAREX CRAWEI Dewey E C
Shore of Lake Huron, 1929 (L S Ehlers)

CAREX LACUSTRIS Willd (*C riparia* W Curtis) E C
Along Bessey Creek, 1929 (L S Ehlers)

31 POACEAE (Grass Family)

BROMUS INERMIS LEYSS Awnless Brome Grass E C
A grass now thoroughly established and extending its area rapidly in the southeastern corner of Black Lake and in Burt Township near Mullet Lake

AGROPYRON DASYSTACHYUM (Hook) Vasey E C
Pries' Landing, Lake Huron, 1929

35 IRIDACEAE (Iris Family)

IRIS LACUSTRIS Nutt E C
Shore of Lake Huron at Pries' Landing, 1929

45 ORCHIDACEAE (Orchid Family)

LIMNORCHIS DILATATA (Pursh) Rydb (*Habenaria dilatata* (Pursh) Gray) E C
In the Thuja woods at Mud Lake Bog, 1928

60 RANUNCULACEAE (Crowfoot Family)

ANEMONE HUDSONIANA Richards (*Anemone multifida* Poir) E C
Shore of Lake Huron south of Mackinaw City, 1929

105 CALLITRICHACEAE (Water Starwort Family)

CALLITRICHE PALUSTRIS L E C
Roadside ditch (U S Highway 23) north of Cheboygan and in a creek east from Van, 1929

108 HYPERICACEAE (St John's-wort Family)

HYPERICUM KALMIANUM L E C
Shore of Lake Huron at Pries' Landing, 1929

126 PAPAVERACEAE incl FUMARIACEAE

BICUCULLA CANADENSIS (Goldie) Millsp (*Dicentra canadensis* (Goldie) Walp) E C
In beech-maple forests on Colonial Point and at Mud Lake, 1926

132 BRASSICACEAE (Mustard Family)

CONRINGIA ORIENTALIS (L) Dumort F C
A weed in the experimental bird pens at the Biological Station, 1928 (Helen R Coburn and Doris Dean)

133 CARYOPHYLLACEAE (Pink Family)

ARENARIA STRICTA Michx E C
Abundant in swampy area in jack-pine plains south of Burt Lake, 1928

135 PORTULACACEAE (Purslane Family)

CLAYTONIA CAROLINIANA Michx E.C
Abundant in a beech-maple forest near Mud Lake, 1926

169 BORAGINACEAE

LITHOSPERMUM CAROLINENSE (Walt) MacM (*L Gmelini* (Michx) Hitchc) E C
Jack-pine plains south of Burt Lake, 1928

175 GENTIANACEAE (Gentian Family)

GENTIANA PROCERA Holm E C
Shore of Lake Huron, Pries' Landing, 1929, abundant

178 SCROPHULARIACEAE (Figwort Family)

CHAENORRHINUM MINUS (L) Lange (*Linaria minor* (L) Desf) E C
Railway ballast at Mackinaw City and on rubble at Black Lake, 1928

AGALINIS PAUPERCULA (A Gray) Britton (*Gerardia paupercula* (Gray) Britton) E C
Shore of Lake Huron, Pries' Landing, 1929

192 ROSACEAE (Rose Family)

OPULASTER OPULIFOLIUS (L) Kuntze (*Physocarpus opulifolius* (L) Maxim) E C
Shore of Lake Huron, Pries' Landing, 1929

199 FABACEAE (Pea Family)

MELILOTUS OFFICINALIS (L) Lam E C
Field and roadside, Riggsville and Cheboygan

200 SAXIFRAGACEAE (Saxifrage Family)

PARNASSIA CAROLINIANA Michx E C
Shore of Lake Huron at Pries' Landing, 1929

PARNASSIA PARVIFLORA DC E C
Shore of Lake Huron, Pries' Landing, 1929

204 DROSERACEAE (Sundew Family)

DROSERA LINEARIS Goldie E C
On the mat surrounding Blanchard Lake, 1929

276 APIACEAE (Carrot Family)

DAUCUS CAROTA L — E C
Roadside, near Nigger Creek and abundant along roads near Cheboygan

278 RUBIACEAE (Madder Family)

GALIUM ASPRELLUM Michx — E C
Thickets and low woods along Nigger Creek, Burt Township, 1929

287 HELIANTHACEAE

HELIANTHUS MAXIMILIANI Schrad — E C
Ruderal on the Topinabee Road near Crumps, 1929

COREOPSIS LANCEOLATA L — E C
Shore of Lake Huron at Pries' Landing, 1929

296 ANTHEMIDACEAE

ARTEMISIA CAUDATA Michx — E C
A hairy form in the jack-pine plains south of Burt Lake and normal plants along Lake Huron at Pries' Landing.

ARTEMISIA ANNUA L Wormwood — E C
Weed on sawdust pile at mill ruins at Wolff's Bog, 1929

298 CARDUACEAE

CARDUUS CRISPUS L — E C
A ruderal along the Cheboygan Road in Inverness Township, 1928

In the list published by the authors in 1924, some of the records for Emmet County were based solely on an unpublished list of Emmet County plants by Fallass and Swift Such species were indicated by "E *" During the last three summers the presence of the following species in Emmet County has been verified by collections of our own

Phylum PTERIDOPHYTA

4 OSMUNDACEAE (Royal Fern Family)

OSMUNDA CLAYTONIANA L — E C
In bog woods bordering Larks Lake, 1929

Phylum CALAMOPHYTA

2 Equisetaceae (Horsetail Family)

Equisetum laevigatum A Br E C
Little Traverse Bay, 1923

Phylum ANTHOPHYTA

6 Sparganiaceae (Bur-Reed Family)

Sparganium angustifolium Michx E C
French Farm Lake, 1928

30 Cyperaceae (Sedge Family)

Eleocharis tenuis (Willd) Schultes E C
In marshy margin of Wycamp Lake, 1929

31 Poaceae (Grass Family

Poa nemoralis L E C
Woods at Harbor Point, 1925
Panicum implicatum Scribn E C
In the aspens near French Farm Lake, 1928

45 Orchidaceae (Orchid Family)

Cypripedium acaule Ait E C
Coniferous woods near Big Stone Bay
Limodorum tuberosum L (*Calopogon pulchellus* (Sw) R Br) E C
Little Traverse Bay, also seen at Harbor Point

71 Malvaceae (Mallow Family)

Malva moschata L Musk Mallow E C
Roadside herb south of Carp Lake, 1929

81 Urticaceae

Humulus Lupulus L Hops E C
Vine near abandoned dwellings, west of Pellston, 1929

108 HYPERICACEAE (St John's-wort Family)

HYPERICUM PERFORATUM L E C
Pasture near Cross Village, 1918

132 BRASSICACEAE (Mustard Family)

SINAPIS ARVENSIS L (*Brassica arvensis* (L) Kuntze) E C
A weed in the mill yard at Pellston, 1928

ARMORACIA ARMORACIA (L) Britton (*Radicula Armoracia* (L) Robinson) Horseradish E C
Roadside ditch near Levering, 1929

ARABIS BRACHYCARPA (T & G) Britton E C
In thickets near Bliss, 1929

140 SALICACEAE (Willow Family)

SALIX PEDICELLARIS Pursh Bog Willow E C
Shrub in a *Carex lasiocarpa* bog north of Wycamp Lake, 1929

160 PYROLACEAE (Wintergreen Family)

PYROLA AMERICANA Sweet E C
Coniferous woods in Big Stone Bay, 1927

PYROLA ULIGINOSA Torr (*Pyrola asarifolia* var *incarnata* (Fisch) Fernald) E C
Cleared Thuja woods, Little Traverse Bay, 1923

167 CONVOLVULACEAE (Morning Glory Family)

CONVOLVULUS ARVENSIS L Field Bindweed E C
A ruderal south of Van The patch is reported to be in its fourth year and extending vigorously, 1928

169 BORAGINACEAE (Borage Family)

CYNOGLOSSUM OFFICINALE L E C
A weed in the mill yard at Pellston, 1928, and at Cecil Bay

171 SOLANACEAE (Potato Family)

PHYSALIS HETEROPHYLLA AMBIGUA (A Gray) Rydb Ground Cherry E C
Field weed west of Pellston, 1929

178 SCROPHULARIACEAE (Figwort Family)

VERONICA AMERICANA Schwein F C
Wet stony point in Big Stone Bay

191 LAMIACEAE (Mint Family)

MENTHA PIPERITA L E C
Cold streams and springy soil in Little Traverse Bay, 1923

262 ACERACEAE (Maple Family)

ACER SACCHARINUM L (Soft Maple) E C
Planted in Pellston

269 JUGLANDACEAE (Walnut Family)

JUGLANS NIGRA L Black Walnut E C
Planted west of Brutus, 1929
JUGLANS CINEREA L Butternut E C
Planted near Alanson and near Cross Village, 1929

271 FAGACEAE (Beech Family)

QUERCUS ALBA L White Oak E C
Trees in woods west of Brutus, 1929

292 INULACEAE

ANTENNARIA PLANTAGINIFOLIA (L) Richards E C
Herb in piny aspens east of Pellston, 1927

293 ASTERACEAE

ERIGERON ANNUUS (L) Pers Daisy Fleabane E C
Ruderal herb north of Larks Lake, 1929

296 ANTHEMIDACEAE

TANACETUM VULGARE L Tansy E C
Roadside herb near Canby P O , 1929
ARTEMISIA ABSINTHIUM L Absinth E C
Roadside herb near Canby P O , 1929

300 LACTUCACEAE

LACTUCA SAGITTIFOLIA Ell E C

A weed in ballast of the Grand Rapids and Indiana Railroad, north of Carp Lake, 1928

TABLE OF SPECIES

Families	Emmet County	Cheboygan County	Total
Phylum 9 PTERIDOPHYTA			
1 Ophioglossaceae	2	8	8
3 Isoetaceae	0	2	2
4 Osmundaceae	3	3	3
11 Polypodiaceae	11	20	20
Phylum 10 CALAMOPHYTA			
2 Equisetaceae	12	12	13
Phylum 11 LEPIDOPHYTA			
1 Lycopodiaceae	5	6	6
3 Selaginellaceae	2	2	3
Phylum 13 STROBILOPHYTA			
3, 5, 6. Pinaceae	11	11	11
9 Taxaceae	1	1	1

TABLE OF SPECIES

Phylum 14 ANTHOPHYTA

	Families	Emmet County	Cheboygan County	Total
1	Alismataceae	4	4	5
4	Scheuchzeriaceae	2	3	3
5	Typhaceae	1	1	1
6	Sparganiaceae	6	6	8
9	Potamogetonaceae	10	16	16
10	Liliaceae	19	22	23
12	Pontederiaceae	1	0	1
18	Juncaceae	13	10	13
19	Eriocaulonaceae	1	1	1
22	Naiadaceae	0	1	1
24	Araceae	2	4	4
25	Lemnaceae	1	3	3
30	Cyperaceae	91	105	115
	(Carex)	(68)	(79)	(86)
31	Poaceae	81	93	103
32	Hydrocharitaceae	4	4	4
35	Iridaceae	4	3	4
45	Orchidaceae	31	35	36
60	Ranunculaceae	25	26	28
62	Berberidaceae	1	2	2
67	Ceratophyllaceae	0	1	1
71	Malvaceae	3	4	4
76	Tiliaceae	1	1	1
79	Ulmaceae	1	1	1
80	Moraceae	1	1	1
81	Urticaceae	2	4	4
82	Sarraceniaceae	1	1	1
84	Geraniaceae	1	2	2
85	Oxalidaceae	3	1	3
87	Balsaminaceae	2	2	2
89	Linaceae	1	1	1
101	Polygalaceae	1	2	2
104	Euphorbiaceae	7	4	8
106	Callitrichaceae	1	1	1
107	Cistaceae	1	2	2
108	Hypericaceae	4	7	8
118	Violaceae	11	14	15
126	Papaveraceae	5	2	5
128	Nymphaeaceae		4	4

TABLE OF SPECIES (*Continued*)

Phylum 14 ANTHOPHYTA

Families		Emmet County		
132	Brassicaceae	32	37	41
133	Caryophyllaceae	16	19	21
135	Portulacaceae	3	3	3
136	Aizoaceae	1	1	1
140	Salicaceae	17	24	25
145	Amaranthaceae	4	3	4
146	Chenopodiaceae	6	6	6
147	Polygonaceae	20	23	25
148.	Nyctagineaceae	0	1	1
151	Primulaceae	4	4	5
152	Plantaginaceae	3	5	5
157	Ericaceae	17	17	18
160	Pyrolaceae	8	8	8
166	Polemoniaceae	0	1	1
167	Convolvulaceae	3	4	4
168	Hydrophyllaceae	1	0	1
169	Boraginaceae	11	13	14
171	Solanaceae	6	8	9
172	Oleaceae	4	5	5
175	Gentianaceae	5	5	6
176	Apocynaceae	2	5	5
177	Asclepiadaceae	2	4	4
178	Scrophulariaceae	18	17	20
179	Bignoniaceae	1	0	1
182	Orobanchaceae	1	2	2
185	Lentibulariaceae	5	4	5
189	Phrymaceae	0	1	1
190	Verbenaceae	2	3	4
191	Lamiaceae	21	25	27
192	Rosaceae	33	32	38
193	Malaceae	9	13	13
194	Prunaceae	5	7	7
199	Fabaceae	15	23	25
200	Saxifragaceae	4	4	5
202	Grossulariaceae	9	7	10
203	Crassulaceae	2	2	3
204.	Droseraceae	4	3	4
211	Hamamelidaceae	1	1	1
215	Lythraceae	1	1	1
223	Oenotheraceae	10	11	12

TABLE OF SPECIES (*Continued*)

Phylum 14 ANTHOPHYTA

Families	Emmet County		
224. Halorrhagidaceae	4	5	5
232 Cucurbitaceae	1	3	3
236 Rhamnaceae	1	3	3
237 Vitaceae	2	2	2
238 Celastraceae	1	2	2
240 Aquifoliaceae	2	2	2
250 Thymelaeaceae	1	1	1
252 Elaeagnaceae	1	1	1
254 Santalaceae	2	2	2
258 Loranthaceae	1	1	1
262 Aceraceae	6	6	6
268 Anacardiaceae	3	3	3
269 Juglandaceae	2	2	2
270. Betulaceae	7	7	7
271 Fagaceae	5	5	5
272 Myricaceae	1	2	2
275 Araliaceae	3	4	4
276 Apiaceae	12	14	16
277 Cornaceae	7	7	7
278 Rubiaceae	7	13	13
279 Caprifoliaceae	14	14	15
281 Valerianaceae	2	2	2
283 Campanulaceae	6	10	10
287 Helianthaceae	11	15	17
288. Ambrosiaceae	5	3	5
289 Heleniaceae	1	1	1
292 Inulaceae	7	9	9
293 Asteraceae	27	30	32
295 Eupatoriaceae	3	4	4
296 Anthemidaceae	10	11	14
297 Senecionidaceae	4	4	4
298. Carduaceae	7	10	10
300 Lactucaceae	16	21	22
(287–300 "Compositae")		(108)	(118)

SUMMARY OF PHYLA

Phyla	Emmet County	Cheboygan County	Total
9 Pteridophyta	16	33	33
10 Calamophyta	12	12	13
11 Lepidophyta	7	8	9
13 Strobilophyta	12	12	12
14 Anthophyta	834	965	1060
Monocotyledoneae	(271)	(311)	(341)
Dicotyledoneae-Axiflorae	(288)	(331)	(368)
Dicotyledoneae-Calyciflorae	(275)	(323)	(351)
Totals	881	1030	1127

DISPERSAL BY INDIANS A FACTOR IN THE EXTENSION OF DISCONTINUOUS DISTRIBUTION OF CERTAIN SPECIES OF NATIVE PLANTS

MELVIN R GILMORE

WHEN we contemplate a species of plant life I suppose we all think of it in relation to some designated area or areas of the earth's surface which we call the range of the species If we find a species to have continuous distribution over a given area, however extended that area may be, we can think of the probable specific origin in some part of its present range, which we may call the area of characterization Then we shall think of the migration of the species from its original area of characterization until it has populated the entire area of its present range If this distribution be continuous we can picture the migration as having been accomplished by means of the plant's own means of dissemination, whether these means be adaptations for seed dispersal by wind, water or organic agencies, such as mammals, birds and so forth

But if the range of a species is discontinuous we shall find natural barriers in some form intervening between the several areas of distribution and preventing the dissemination of the plant by its usual means of migration Such instances of invasion of new territory beyond natural barriers have occurred in the case of many of our domesticated plants Having been helped over barriers by some agency other than the plant's own means of natural dispersal, it has found itself in a happy situation in which it has been able to disseminate itself again by its own natural adaptations In such situation it has escaped captivity and control, has possessed itself of new territory, and has proceeded to form a new range, effectually separated from the original range though it be and remain

But sometimes these immigrants, even though able to maintain themselves in a locality into which they have been introduced by such extraordinary means, do not find themselves able to extend their invasion greatly Some isolated colonies of certain species of native American flora have come under my observation in a number of localities These colonies have every appearance of having become established by other than ordinary means in the localities where they are now found I shall give a few instances and suggest the factor which appears to me to have been active in the original introduction of these species into the stations where they are found, out of contact with the range of their species, beyond barriers insuperable by the plant's ordinary means of dissemination

Taking the species in taxonomic order and beginning with the lowest, I shall cite first the case of *Acorus calamus*, commonly called calamus or sweet-flag This plant is very common continuously throughout the Atlantic Coast region, along the borders of streams and other wet situations Farther inland it is found less and less frequently Calamus is a plant which very seldom blooms, and I have never known it to produce seeds, so that it is not adapted to disseminate itself or invade new territory But it is found in certain places all the way from Canada to Texas, all these places being at considerable distance from any other stations of the species

There is a large field of *Acorus calamus* in the low ground in the great bend of the Mouse River in the northern part of North Dakota, not far from the village of Towner in that state About five hundred miles away to the south, on Minichadusa River, near the south boundary of South Dakota, there is another patch of calamus There are other patches farther to the south in the state of Nebraska on the Calamus River, on the branches of the Loup River, on the Platte and on the Republican River In Kansas there are patches in places on the Republican, the Kansas, the Arkansas and other rivers In Oklahoma also there are various patches on certain streams

Acorus calamus is a plant very highly valued by Indians for medicinal and other uses All the places which I have mentioned above as stations of this plant are well known to the people of the tribes in those regions And all these stations are in localities formerly much frequented by them They either are in the vicinity of old village sites, or are located near camping places on old Indian trails My opinion is that every one of these patches had its origin by intentional planting long ago by Indian medicinemen I believe that the plant was brought from the Atlantic seaboard and established by stages until it reached the Plains Region, where it is now found in these isolated stations

The next instance I have to offer is that of *Juglans nigra* I was informed of the existence of a grove of black walnut trees in southern Nebraska, in the valley of a tributary of the Little Blue River, at a distance of one hundred and fifty or two hundred miles beyond the range of the species It is said that this grove was there when white men first came to that valley, and according to tradition it had been planted by Pawnee Indians who formerly had villages in the vicinity The Pawnees were always intensive agriculturists The only reasonable explanation of the existence of this isolated station of *Juglans nigra* is that it had been planted by the Pawnees from stock which they had imported from the country of the Otos along the Missouri River to the eastward, and this explanation also agrees with the tradition and with the fact of the high value in which nuts were held by Indians as an item of food

In the country of the Ponkas in northeastern Nebraska there is a station of *Malus ioensis*, the prairie crab-apple, on a small stream which falls into the Niobrara River This location is about two hundred miles beyond the northwest periphery of the range of *Malus ioensis* The Ponkas recognised the presence of this colony of the species here so far out of its natural range as being something unusual, and they call the stream by a name which means "the creek where apples abound" The reasonable explanation of the existence of this isolated colony would seem to be that it had resulted from a visit at some time of Ponkas to the country of the Iowas or the Otos or the Missouris, and the importation of a quantity of the apples with them when they returned home, and that the seed of some of these became established and have since maintained themselves

The four tribes of the Pawnee confederacy were removed by the United States federal government from their own home country in Nebraska to Oklahoma in 1873, because the Pawnee land in Nebraska was desired by white people In the places where they were temporarily settled for the first year of their residence in Oklahoma there may now be seen many thickets of *Prunus americana*, the wild plum, which abounds in the region of the Pawnee country in Nebraska Pawnees, as also other tribes, made much use of all the wild fruits, including wild plums They were used in the fresh state, and quantities were dried to preserve them for future use Pawnees have told me that the plum thickets which now appear in the places where they lived in Oklahoma, when they first came from Nebraska, are the results of the seeds which they threw out after using the dried plums which they had brought in their food provision from Nebraska

The natural range of the buffalo-berry (*Shepherdia argentea*) east of the Rocky Mountains is from Saskatchewan to Nebraska It is commonly found in North Dakota and South Dakota west of the Missouri River In North Dakota its natural range is limited on the east by the Plateau du Missouri, and in South Dakota the eastern limit of its natural range is the Coteaux du Prairie But in certain places in both North Dakota and South Dakota far to the east beyond its natural range a few isolated colonies of buffalo-berry are found

In aboriginal Indian times a regularly traveled trail ran from the woodland region of the upper lakes westward across the Red River of the North, by way of the Pembina River, the Turtle Mountain, the great bend of the Mouse River, then through the Coteaux, across the Plateau du Missouri into the buffalo country of the Missouri River, in the range of *Shepherdia argentea* Another trail from the woodland region out into the Missouri River country led a little farther south across the Red River of the North, westward across the headwaters of the Sheyenne River, and of the James River, and then the Coteaux Another trail of east and west travel, to the Missouri River and return, was farther south, crossing the Red River of the North about where Fargo is now, the Sheyenne where Valley City is, and the James River about where Jamestown is Another trail was still farther south, past Big Stone Lake, then through the lake region of what is now South Dakota and over the Coteaux du Prairie to the Missouri River region On all those lines of old-time Indian travel there are isolated stations of *Shepherdia argentea* at places from one hundred to two hundred miles east of the natural barriers which limit the eastern periphery of the range of the species Such stations are found at the crossings of the upper courses of the James River and the Sheyenne River At the old Sheyenne River crossing where Valley City now stands there is a clump of buffalo-berries And near Milbank, in northeastern South Dakota, not far from the Minnesota state line, in the vicinity of Big Stone Lake, there are some buffalo-berry bushes It is my opinion that all these stations of *Shepherdia* have resulted from seeds becoming established at camping places on the trail, from dried buffalo-berries which Chippewas were taking home with them on return journeys from the Missouri River

Concerning *Nicotiana rustica* the statement is made in Britton and Brown's *Manual of the Flora of the Northern States and Canada* that it is found "in fields and waste places" in Ontario and in the northern and eastern states I have not myself seen it in such situations, but it may be so If it be so, it must be that these vestiges are relicts from the former cultivation of *Nicotiana rustica* by the former Indian inhabitants in the vicinity where they at present occur, for the natural range of *Nicotiana rustica* is in Mexico, many hundreds of miles away from any of these places where it is claimed that it still survives

I have given but a few examples of the sporadic distribution of certain species and the circumstances of their existence, for the purpose of calling attention to what I believe is the means by which these colonies have become established where they are found I think the agency responsible for the establishment of these isolated stations is the human factor, the operation of the Indian people, in some cases purposive, but not so in all I think some colonies were established by purposeful transportation and careful transplantation, in other cases, I think the dissemination was by chance, but in all the given examples cited I think that the transportation was by human agency

I am sure there must be many other instances which might be shown of similar import to the few which I have given, and I should be very glad if any of my readers would bring to my attention any similar examples of which they may have knowledge, with all the pertinent facts which are available

UNIVERSITY OF MICHIGAN

GROWTH STUDIES ON FRUITS

THE EFFECT OF THE REMOVAL OF ALTERNATE FLOWER CLUSTERS ON THE DEVELOPMENT OF FRUITS IN THE TOMATO *

FELIX G GUSTAFSON AND HARLOW E LAING

IN THE summer of 1928, two hundred vigorous and uniform tomato plants were selected for an experiment on the effect on setting and development of fruits of isolating fruit clusters from one another by girdling the stem These plants were all pruned to one stem and also had the first inflorescence removed as soon as it was formed They were divided into four groups of fifty plants each The plants of each group were uniformly distributed throughout the field by arranging them according to the following scheme A1, B1, C1, D1, A2, B2, C2, D2, A3, etc In this way the soil and cultural conditions were uniform for all sets

The four sets were treated as follows Set A, control, B the same as A, except that besides the first flower cluster, the third, fifth and seventh were also removed, C the same as A, except that the stem was girdled directly above each inflorescence, D like C, but the girdling was done just above the second leaf above each flower cluster After a few weeks it became evident from both gross and microscopic examination that the girdling was not effective, i e new cambium and phloem were formed, and hence the two sets of girdled plants were no longer used in this experiment Groups A and B were continued, however, as a study of the effect on fruiting of the removal of alternate inflorescences

Before the results of this study are taken up one may first note the general results obtained when plants were pruned to one stem instead of being permitted to branch freely The plants kept rigidly to one stem had much thicker and taller stems than those not pruned. Their individual fruits were considerably larger and

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* Paper from the Department of Botany of the University of Michigan, No 339

in many plants the apex of a fruiting cluster would proliferate, i e form a stem with several leaves This practically never happens when the plants are permitted to branch freely It was found that at least two buds were formed in the axil of each leaf and sometimes three These were formed successively, after one had been removed a second one and sometimes a third would develop, but never more Pruning to one stem would be economical only if ground were at a premium or if one were desirous of producing extraordinarily large fruits The total yield of fruits per plant is undoubtedly less when it is pruned to one stem than when branching is permitted This statement is, however, based on general observations rather than on exact measurements

The results produced by removing every other cluster of fruit buds can be best brought out by tables

TABLE I

NUMBER OF FRUITS SET PER CLUSTER

Cluster no	Average number of fruits set per cluster		Percentage increase in setting
	Plants A	Plants B	
2	5 74	5 62	
3	5 86		
4	5 30	6 13	15 7
5	5 18		

TABLE II

NUMBER OF FRUITS DEVELOPED PER CLUSTER

Cluster no	Average number of fruits developed per cluster		Percentage increase in development
	Plants A	Plants B	
2	4 26	4 67	9 6
3	3 46		
4	1 98	4 04	104 0
5	1 34		
6	1 50	3 45	130 0

TABLE III

Percentage of Development of Fruits

Cluster no	Fruits developed as percentage of setting		Percentage increase in development
	Plants A	Plants B	
2	74 2	81 5	9 1
3	59 0		
4	37 4	68 5	83 2
5	39 2		

TABLE IV

Average Weight of Individual Fruits

Cluster no	Average weight of individual fruit in grams		Percentage increase in weight per fruit
	Plants A	Plants B	
2	159 4	153 3	− 3 7
3	168 3		
4	154 8	184 8	19 8
5	130 6		
6	88 3	110 5	25 1

TABLE V

Total Yield of Fruit per Cluster

Cluster no	Total yield in grams per cluster		Percentage increase in yield
	Plants A	Plants B	
2	33,953	35,104	3 4
3	29,118		
4	15,279	36,389	138 1
5	8,750		
6	6,716	18,676	178 1
7–10	5,530		
8–10		4,359	
Total yield 50 plants	99,346	94,528	

The tables show that, if only every other inflorescence is permitted to fruit, the number of fruits setting per inflorescence will be slightly increased, the number of fruits actually developing per cluster will be more than doubled, and these fruits will be larger All three conditions tend to increase the yield and as a result the corresponding clusters on the experimental plants will bear a greater amount of fruit This larger yield per cluster is so great that, although these plants have only about half as many clusters as the control plants, yet the total yield is 95.15 per cent of that of the control plants

It will be noted that in cluster 2, Table I, the setting is slightly less in the experimental plants than in the control The setting in these inflorescences was of course completed before the next inflorescence was removed, so that no effect could be expected Even though the setting was somewhat smaller, yet the number of fruits developing was 9 1 per cent higher than in the control plants The removal of fruiting cluster 3 was operative in this development

In Table II it is noticed that the control plants produce fewer and fewer fruits per inflorescence as the plant ages Though this is also true in the experimental plants, the decrease is very much less In Table V another fact is brought out with reference to the decrease in productivity of the later developed inflorescences The control plant produced less than one half as much fruit in cluster 4 as in 2, while the experimental plant actually produced more in cluster 4 than in 2

The decrease in the productivity of the later developed flower clusters is undoubtedly due, as explained in a previous paper (1), to a decrease in available nutrient material. When all the blossoms are permitted to develop, the number of fruits set in the early formed flowers will be so large that they will use up nearly all the nutrient material, either produced in the plant or coming into it, leaving very little for those produced later, and as a consequence fewer will develop and they will be small On the other hand, those plants from which some inflorescences are removed have as much nutrient material as the control plants, but many fewer flowers and fruits to support There is no reason to suppose that the experimental plants do not photosynthesize as much as the others, or that their roots are not as active in absorption Therefore the experimental plants produce more and larger fruits per fruiting cluster than the controls, because there are fewer clusters to support and not, as many investigators have claimed, because of the production of inhibiting substances in the controls If inhibiting substances were formed, it seems impossible that eight to ten fruits would develop in a single cluster, which is what sometimes happens in the experimental plants This was never found in the control plants By nutrient material is meant the food-supply, mineral material, water, oxygen and any other material used in building up and maintaining the cells

It is believed that these experiments give further proof for the contention of the senior author that growth is limited by nutrient conditions of a plant rather than by the formation of inhibiting substances, as claimed by many investigators

University of Michigan

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LICHENS FROM THE STATE OF OKLAHOMA *

JOYCE HEDRICK

SO FAR as the writer has been able to ascertain, no work has been published on lichens collected in the state of Oklahoma, nor are there any collections from this state to be found in the herbaria of the University of Michigan, the University of Oklahoma, the Sullivant Moss Society or the private one of C C Plitt

The material from which this list was made was collected by Robert E Stratton over a period of three years, 1927–29, in the following counties Delaware, Mayes, McCurtain, Johnston, Murray, Payne, Osage, Kay, Harmon, Roger Mills and Cimarron The counties represented indicate a state-wide survey, yet in many of them but few specimens were collected, so that further collecting is much to be desired

The collection numbered 106 specimens, representing 59 species and subspecies in 22 genera Of these, 44 species are more or less widely distributed over the United States, 4 are common east of the Rocky Mountains, 4 are limited to the United States west of the Mississippi River, 3 are common in northern United States and rare southward, 3 are limited to the Great Plains region, and 1 has been found only in Nebraska (2, 3, 5, 6) A majority of the specimens are of crustose form and a large number grow on rocks Of the 59 species and subspecies 38 are crustose, 13 foliose and 8 partly or wholly fruticose Also, 29 were collected on rocks, 7 on soil, 22 on trees and 1 on old wood

The pyrenomycetous lichens are represented in this list only by *Staurothele umbrina* (Ach) Tuck This does not mean that there are no other pyrenomycetous lichens in the state, but rather that they have been overlooked by the collector The same statement may be made of the lichens belonging under Hysteriales, represented here by *Opegrapha varia* Pers

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* Paper from the Herbarium of the University of Michigan, No 14

The most conspicuous genera are those of crustose form The genus Caloplaca, with a more or less plectenchymatous thallus and a heavy thalloid exciple, is represented by 8 species The genus Lecanora, also with a heavy thalloid exciple, has 9 species and 2 subspecies in this list Both these genera are very common throughout the United States and are well represented in the drier regions of the Southwest (1) Of the foliose forms, the genera Physcia and Parmelia are the most common Parmelia is represented by 6 species and Physcia by 4 The genus Cladonia found in such profusion throughout northern United States is represented here by 3 species and 1 subspecies, all very small specimens

Oklahoma is one of the southwestern states of the Great Plains region Its elevation varies from sea-level along the Arkansas River in the central-eastern part, rising slowly to 1000 and 1500 feet throughout the central part, to 2000 feet in the western part and 4000 feet in the far western county of Cimarron Four regions of vegetation are found within the state The southeastern and extreme eastern portion lies in the region of the Deciduous Forest, the eastern and central portion in the Grasslands-Deciduous Forest Transition, the western portion in the region of Grasslands, and the western end of the panhandle in the region of Desert-Grasslands Transition (4, Pl I) The precipitation for the state varies from 40 to 50 inches in the southeast, 30 to 40 throughout the eastern and central part, 20 to 30 in the western and 10 to 20 in the far west (4, p 280)

The classification of A Zahlbruckner (7) has been followed unless otherwise indicated The specimens are deposited in the Herbarium of the University of Michigan.

The distribution in states other than Oklahoma has been checked against the distribution records of the late Dr Bruce Fink

VERRUCARIACEAE

Staurothele umbrina (Ach) Tuck — On soft blue sandstone, Stillwater, Payne County, January 1, 1927 On rocks from New England to Florida and westward to the Rocky Mountains

GRAPHIDACEAE

Opegrapha varia Pers — On oaks at Price's Falls, Arbuckle Mountains, Murray County, April 22, 1927 On trees throughout the United States

LECIDEACEAE

Bacidia schweinitzii (Tuck) Fink — On bark of dead hickory, Broken Bow, McCurtain County, May 16, 1929 On trees in eastern United States and westward to Texas

Biatorella simplex (Dav) Br & Rostr — On white sandstone on high hill, Stillwater, Payne County, March 3, 1929 On rocks throughout the United States.

Buellia[1] **myriocarpa** (Lam & DC) Mudd — On sandstone, Stillwater, Payne County, February 24, 1927, and March 5, 1927 On old wood and rocks throughout the United States

Buellia parasema (Ach) Koerb — On red oak recently fallen, Dripping Springs, Delaware County, July 17, 1929 On trees throughout the United States

Buellia spuria (Schaer) Arn — On red sandstone on high hill, Stillwater, Payne County, March 3, 1929, on quartz rock, Cherokee Lake, Salina, Mayes County, July 17, 1929 On rocks throughout the United States

Lecidea lapicida Ach — On sandstone, Price's Falls, Murray County, May 11, 1929 On rocks in Maine, Minnesota, South Dakota and southern California

Lecidea parasema Ach — On sandstone, Kenton, Cimarron County, June 16, 1929 On rocks throughout the United States

Lecidea speirea Ach — On limestone, Turner Falls, Murray County, May 10, 1929 On rocks in New England, West Virginia, Minnesota, Wyoming, Idaho, Washington and California

Psora crenata (Tayl.) Reinke — On limestone on barren hill, Ravia, Johnston County, September 7, 1927 On soil and rocks in Texas, New Mexico, Arizona, Colorado and Montana

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[1] Under Buelliaceae in classification by Zahlbruckner

PSORA DECIPIENS (Ehrh) Hoffm — On soil, Hollis, Harmon County, August 6, 1927 On soil throughout the United States except in the extreme southern part

PSORA ICTERICA (Mont) Müll Arg — On soil on top of rocky clay hill, Stillwater, Payne County, February 23, 1927, and April 18, 1929 On soil in New York and throughout the United States west of the Mississippi River

PSORA RUSSELLII (Tuck) Schneid — On sandstone of a dry rocky hill, Stillwater, Payne County, February 8, 1926, January 1, 1927, and March 3, 1929, on limestone rocks and red sandstone, Price's Falls, Murray County, April 30, 1926, April 22, 1927, and May 11, 1929, on limestone rocks, Kaw City, Kay County, April 20, 1929 On rocks throughout the United States

CLADONIACEAE

CLADONIA CRISTATELLA Tuck — On soil at top of hill, Dripping Springs, Delaware County, July 18, 1929 On soil throughout the United States east of the Rocky Mountains

CLADONIA FURCATA (Huds) Schrad — On soil, Dripping Springs, Delaware County, May 4, 1928, and July 17, 1929 On soil, frequently over rocks and rarely on old wood throughout the United States

CLADONIA PYXIDATA (L) Hoffm — On sandstone among mosses in a ravine of open wood, Stillwater, Payne County, January 30, 1929, on mossy rocks on north slope, Ripley, Payne County, April 25, 1929 On soil or rotten wood throughout the United States

CLADONIA PYXIDATA (L) Hoffm CHLOROPHAEA (Spreng) Floerke — On rocky bank in a wood, and on soil over old grapevine, Dripping Springs, Delaware County, July 17 and 18, 1929, on mossy hillside in a wood, Cherokee Lake, Salina, Mayes County, July 17, 1929 On soil or rotten wood throughout the United States

PELTIGERACEAE

Peltigera polydactyla (Neck) Hoffm — On soil, Dripping Springs, Delaware County, July 18, 1929 On soil throughout the United States

ACAROSPORACEAE

Acarospora citrina (Tayl.) Zahlbr — On basalt rock, Black Mesa, Kenton, Cimarron County, June 16, 1929 On rocks throughout the United States

LECANORACEAE

Candelariella vitellina (Ehrh) Müll Arg — On basalt rock, Black Mesa, Kenton, Cimarron County, June 16, 1929 On rocks and old wood throughout the United States

Lecanora atra (Huds) Ach — On sandstone, Price's Falls, Murray County, May 11, 1929 On rocks throughout the United States

Lecanora effusa (Pers) Ach — On an oak stump, Stillwater, Payne County, January 1, 1927 On old wood in Nebraska

Lecanora hageni Ach — On red oak, Arbuckle Mountains, Price's Falls, Murray County, April 21, 1928, on an old log, Dripping Springs, Delaware County, May 4, 1928, on black sandstone, Stillwater, Payne County, April 18, 1929, on sandstone, Antelope Hills, Durham, Roger Mills County, July 28, 1929 On trees, old wood and rocks throughout the United States

Lecanora muralis (Schreb) Tuck — On rocks on a northeast slope, Stillwater, Payne County, January 1, 1927 On rocks throughout the United States

Lecanora pallida (Schreb) Schaer — On dead branches possibly swamp maple, Grassy Lake, Broken Bow, McCurtain County, May 14, 1929 On trees throughout the United States

Lecanora rubina (Lam & DC) Ach — On sandstone, Stillwater, Payne County, February 24, 1927 On rocks throughout the United States

Lecanora subfusca (L) Ach — On bark of dead hickory, Broken Bow, McCurtain County, May 16, 1929 On trees or old wood, rarely on rocks or over mosses, throughout the United States

Lecanora subfusca (L) Ach **allophana** Ach — On bark of living ash tree, Price's Falls, Murray County, May 10, 1929 On trees and old wood throughout the United States.

Lecanora subfusca (L) Ach **campestris** Schaer — On sandstone, Fairfax, Osage County, July 12, 1929 On rocks throughout the United States

Lecanora varia (Hoffm) Ach — On bark of living tree, Blackwell, Kay County, April 20, 1929 On trees and rocks throughout the United States.

Lecanora versicolor (Pers) Fink — On conglomerate rock, Arbuckle Mountains, Price's Falls, Murray County, May 11, 1929 On rocks in Iowa, Minnesota, Nebraska, Kansas and Missouri

Urceolaria scruposa (Schreb) Ach — On red sandstone, near Ripley, Payne County, January 13, 1929 On rocks throughout the United States.

PERTUSARIACEAE

Pertusaria communis Lam & DC — On flint rock, Cherokee Lake, Salina, Mayes County, July 17, 1929 On trees and rocks throughout the United States

Pertusaria multipuncta (Turn) Nyl — On living ash bark, Price's Falls, Murray County, May 10, 1929 On trees throughout the United States

PARMELIACEAE

Candelaria concolor (Dicks) Arn — On pecan bark, Stillwater, Payne County, January 1, 1927, on *Bumelia sp*, Stillwater, Payne County, March 3, 1929, on bark of living tree, Price's Falls, Murray County, May 11, 1929 On trees throughout the United States

Parmelia borreri Turn — On oak near Price's Falls, Murray County, April 21, 1928, on bark of living walnut and horse-chestnut, and on dead cedar, Price's Falls, Murray County, May 11, 1929, on *Bumelia sp*, Stillwater, Payne County, March 3, 1929, on red oak, recently fallen, Dripping Springs, Delaware County, July 17, 1929 On trees and, rarely, on rocks throughout eastern United States and westward to the Rocky Mountains

Parmelia caperata (L) Ach — On dead cedar, Price's Falls, Murray County, April 30, 1926, on red oak recently fallen, Dripping Springs, Delaware County, July 17, 1929 On trees, old wood and rocks throughout the United States

Parmelia cetrata Ach — On dead cedar, Price's Falls, Murray County, April 30, 1926, on dead branches, possibly swamp maple, Grassy Lake, near Broken Bow, McCurtain County, May 14, 1929 On trees, old wood and rocks throughout the United States

Parmelia conspersa (Ehrh) Ach — On sandstone, near Fairfax, and near Barnsdall, Osage County, July 12, 1929 On rocks and, rarely, on old wood throughout northern United States and southward in the mountains

Parmelia perforata (Wulf) Ach — On dead ash limb on ground, Price's Falls, Murray County, May 10, 1929, on dead cedar, Price's Falls, Murray County, May 11, 1929, on dead branches, Grassy Lake, Broken Bow, McCurtain County, May 14, 1929 On trees and, rarely, on rocks throughout the United States

Parmelia rudecta Ach — On dead branches, possibly swamp maple, Grassy Lake, Broken Bow, McCurtain County, May 14, 1929 On trees and, rarely, on rocks throughout the United States

USNEACEAE

Ramalina calicaris (L) E Fries — On dead ash limb on ground, Price's Falls, Murray County, May 10, 1929 On trees, old wood and, rarely, on rocks in eastern United States and westward to Nebraska and Minnesota

Usnea florida (L) Web — On oak log, Dripping Springs, Delaware County, May 4, 1928, on dead branches, Grassy Lake, Broken Bow, McCurtain County, May 14, 1929 On trees, old wood and, rarely, on rocks throughout the United States

Usnea florida (L) Web **strigosa** Ach — On red oak recently fallen, Dripping Springs, Delaware County, July 17, 1929 On trees and old wood from Maine to Iowa and southward to New Mexico

TELOSCHISTACEAE

Blastenia[2] **ferruginea** (Huds) Arn — On sandstone, Stillwater, Payne County, February 24, 1927 On trees, old wood and rocks throughout the United States

Caloplaca[2] **aurantiaca** (Lightf) T Fries — On bark of living cottonwood, Stillwater, Payne County, April 9, 1929, on bark of living trees, Price's Falls, Murray County, May 11, 1929 On trees, old wood and rocks throughout the United States

Caloplaca camptidia (Tuck) Fink — On dead branches, possibly swamp maple, Grassy Lake, Broken Bow, McCurtain County, May 14, 1929 On trees and wood throughout eastern United States and westward to Illinois, and in Texas and Oregon

Caloplaca cerina (Hoffm) T Fries — On hard red sandstone and soft blue sandstone, Stillwater, Payne County, January 1, 1927 On rocks, trees and, rarely, on old wood throughout the United States

Caloplaca cinnabarina (Ach) Zahlbr — On hard red sandstone and rocks, Stillwater, Payne County, January 1, 1927, on basalt rock and on sandstone, Black Mesa, Kenton, Cimarron County, June 16, 1929, on sandstone, Antelope Hills, Durham, Roger Mills County, July 28, 1929 On rocks throughout the United States

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[2] Under Caloplacaceae in classification by Zahlbruckner

CALOPLACA CITRINA (Hoffm) T Fries — On sandstone, Antelope Hills, Durham, Roger Mills County, July 28, 1929 On rocks and mortar throughout northern United States and extending southward

CALOPLACA EUGYRA (Tuck) Fink — On conglomerate rocks, Price's Falls, Murray County, May 11, 1929 On rocks in Texas and Colorado

CALOPLACA MURORUM (Hoffm) T Fries — On limestone, Price's Falls, Arbuckle Mountains, Murray County, April 22, 1927, on sandstone, Price's Falls, Murray County, May 11, 1929, on sandstone, Antelope Hills, Durham, Roger Mills County, July 28, 1929 On rocks in northern United States and southward to Arizona

CALOPLACA SIDERITIS (Tuck) Fink — On sandstone, Stillwater, Payne County, January 1, 1927 On rocks in northern United States and, rarely, southward

TELOSCHISTES CHRYSOPHTHALMUS (L) T Fries — On *Bumelia sp* , Stillwater, Payne County, March 3, 1929 On trees and old wood throughout the United States

PHYSCIACEAE

PHYSCIA ADGLUTINATA (Floerke) Nyl — On pecan bark, Stillwater, Payne County, January 1, 1927, on bark of living black walnut, Blackwell, Kay County, April 20, 1929 On trees and shrubs throughout the United States

PHYSCIA OBSCURA (Schaer) Nyl. — On bark of living tree, Price's Falls, Murray County, May 11, 1929 On trees, wood and mosses throughout the United States

PHYSCIA STELLARIS (L) Nyl — On bark of elm, living cottonwood, living black locust, living walnut and *Bumelia sp* , Stillwater, Payne County, January 1, 1927, March 8, 1927, March 3, 1929, April 9, 1929, on rocks, sandstone, dead cedar and living trees, Arbuckle Mountains, Price's Falls, Murray County, April 21, 1928, May 11, 1929 On trees and rocks throughout the United States

PHYSCIA TERETIUSCULA (Ach) Fink — On sandstone, Fairfax, Osage County, July 12, 1929 On rocks in Minnesota, Iowa and North Dakota

UNIVERSITY OF MICHIGAN

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INHERITANCE STUDIES OF WHITE-CAPPING IN YELLOW DENT MAIZE II [*]

CHANDRAKANT G KULKARNI

INTRODUCTION

IN A previous paper (1926) it was shown that white-capping (*Wc*) in dent corns is due to a single Mendelian factor This factor is dominant to yellow-capping (*wcY*) in the first generation and segregates in the second in a 3 1 ratio of white-capped grains to yellow-capped Silver King, a white dent corn (*Wc y*), when crossed to Bailey Connecticut Yellow (*wcY*), gives F_1 ears having all white-capped grains When these F_1 kernels are self-pollinated the next year, a ratio of 9 white-capped 3 yellow 4 white is obtained This shows that Silver King carries a white-capping factor (*Wc*) which is not expressed in the absence of yellow endosperm

White-capped yellow kernels show that the characteristic yellow pigment of the endosperm is entirely lacking in the cap region at the crown This proves that white-capping is a condition of the endosperm brought about by the action of the inhibitor (*Wc*)

PREVIOUS WORK ON THE ENDOSPERM COLORS IN MAIZE

Early studies on the inheritance of endosperm colors in maize were carried on by Correns (1899, 1901) and Lock (1906) As interpreted by these authors, yellow endosperm in maize is determined by the presence of a factor for yellow, in the absence of which endosperm remains white East (1910) and East and Hayes (1911) observed 15 1 ratios and reported two factors for yellow endosperm, each behaving when crossed with its absence as an independent allelomorphic pair These yellows were of a similar nature and they were considered to result from duplicate genes, although the investigators state that it was impossible always to classify pale yellow endosperm seeds correctly On the basis of this work, the inheritance of yellow endosperm color in maize is cited by Shull (1914) and others as one of four characters for which evidence of duplicate genes has been definitely established Emerson (1911) also describes two factors for the yellow endosperm, one for a deep or golden yellow and the other for a pale yellow White (1917) reported a factor for white endosperm (*Wh*)[1] which is dominant to both the deep yellow and pale yellow, but the dominance is not complete Kvakan (1924) described a brown aleurone color (*Bn*) in maize He shows that this brown aleurone is the same as the pale yellow endosperm described by East and Emerson, and concludes that the two yellow colors in the endosperm could not result from duplicate genes, as was supposed by East and Hayes Anderson (1924), working with yellows of various intensity, concluded that there are two endosperm colors in maize, one a dark yellow and the other a pale yellow In addition to the two factors for the yellow endosperm Anderson noted other factors which he classified as modifying factors Hayes and Brewbaker (1926) report three factors for yellow endosperm color The data presented by these authors indicate that all these factors are located in chromosome VIII, as designated by Lindstrom (1923)

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[*] Paper from the Department of Botany of the University of Michigan, No 335.

F_3 AND F_4 DATA OF THE CROSS SILVER KING (*Wc y*) × BAILEY CONNECTICUT YELLOW (*wc Y*)

The F_3 white-capped seeds, when self-pollinated the following year, gave in their progeny 8 ears that had all white-capped kernels, 20 ears gave a ratio of 3 white-capped 1 yellow-capped and 9 ears gave a ratio of 9 white-capped 3 yellow-capped 4 white grains

Fifty-three ears were obtained by self-pollinating the F_3 yellow seeds Thirty-nine of these had all yellow kernels, whereas the remaining 14 gave a ratio of 3 white-capped 1 yellow

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[1] In White's paper this factor was designated as *A*, but since factor *A* is used to denote the color of aleurone and plant in maize (Emerson, 1918, 1921), it was later designated *Wh*.

The white kernels of F_2 generation on self-pollination gave 63 ears and all had white seeds only.

The F_3 data of the cross Silver King (*Wc y*) × Bailey Connecticut Yellow (*wcY*) reviewed above are exactly what should be expected on the basis that white-capping in dent corns is due to a single Mendelian factor.

The F_4 ears obtained from self-pollinating the F_3 kernels of the various phenotypic classes also gave ears which showed that white-capping (*Wc*) is due to a single Mendelian factor.

INHERITANCE OF WHITE-CAPPING IN "DOUBLE-CROSSED BURR LEAMING"

A variety of corn called "Double-crossed Burr Leaming" was received from Dr. D. F. Jones of the Connecticut Agricultural Experiment Station. This corn is white-capped and has lemon-yellow endosperm. These white-capped kernels presumably came from the cross Burr × Leaming. The former is a white corn and the latter a yellow. These kernels on self-pollination gave 30 ears, of which 9 were classified. Seven of them gave a ratio of 1839 white-capped : 595 yellow-capped : 806 white seeds. The deviation from the expected 9 : 7 ratio is 16.5 ± 19.02, and is not significant. A classification of these self-pollinated ears is given in Table I. The 2 remaining ears gave a ratio of 452 white-capped yellow : 158 yellow-capped seeds. The deviation from the expected 3 : 1 ratio is 5.5 ± 7.21. A classification of these two ears is given in Table II. These results indicate that the Burr corn also carries a white-capping factor (*Wc*), which is not expressed in the absence of yellow.

F_3 ears obtained from self-pollinating the seeds of the various F_2 phenotypic classes substantiate the hypothesis that white-capping is due to a single Mendelian factor.

INHERITANCE OF WHITE-CAPPING IN NORTHWESTERN DENT

Northwestern dent corn, with a colored pericarp except in the cap region, was selected for the white endosperm and crossed with Duncan yellow (*wcY*). The F_1 grains from the ears of this cross were all white-capped yellow. When these grains were self-pollinated the following year they gave a ratio of 4902 white-capped 1651 yellow 2021 white seeds The deviation from the expected 9 7 ratio is 79 3 ± 30 95, and is not significant These results are summarised in Table III They indicate that in this case also white-capping is due to a Mendelian factor

INTERRELATIONS OF THE WHITE-CAPPING FACTORS FROM VARIOUS SOURCES

Clement's white cap, which has an orange-yellow under color (*Wc Y*) when crossed to Folk's white cap, which has a lemon-yellow under color, gives in F_1 all white-capped grains The white caps on these F_1 ears are similar to those of the Clement's white cap and Folk's white cap The endosperm of these seeds, however, is lemon-yellow This has been explained by the fact that endosperm is triploid in constitution, the endosperm nucleus of the embryo sac being diploid The reciprocal cross also gives white caps on F_1 indistinguishable from either parent, but the endosperm of these seeds is orange-yellow

Clement's white cap × Connecticut white cap (Double-crossed Burr Leaming) and the reciprocal cross give nothing but the white caps in F_1 These white caps are indistinguishable from those of either parent

Folk's white cap × Connecticut white cap give in F_1 white-capped kernels with lemon-yellow under color The white caps on these F_1 kernels are similar to those of the Folk's white cap on one hand and the Connecticut white cap on the other

The results of the intercrosses between the various varieties of white caps indicate that the white caps of the Clement's white cap, Folk's white cap, Silver King, Burr and Double-crossed Burr Leaming (Connecticut white cap) are phenotypically and genotypically the same

THE RELATION OF THE WHITE CAP TO DOMINANT WHITE ENDOSPERM

Dominant white endosperm × white cap gives in F_1 ears whose seeds are all white-capped A ratio of 1520 white-capped 503 white seeds was obtained from self-pollination of F_1 seeds in a classification of six ears The deviation from the expected 3 1 ratio is 2 75 ± 13 14 and is not significant An analysis of the F_2 seeds of this cross is presented in Table IV

These results show that white-capping is also dominant to the dominant white endosperm in the first generation and segregates in a simple Mendelian ratio in the second

THE RELATION OF THE WHITE CAP TO YELLOW FLINT

In order to determine the relationship of yellow flint, white cap was crossed with it The F_1 ears of this cross had all white-capped seeds Three F_2 ears were obtained by self-pollinating the F_1 white-capped seeds On classification these ears gave 1106 white-capped seeds 380 yellow seeds The deviation from the expected 3 1 ratio is 8 5 ± 11 24 and is not significant The results of the classification of the F_2 seeds are presented in Table V

This shows that white-capping is also dominant to yellow flint in F_1 and segregates in a mono-hybrid ratio in F_2

NOMENCLATURE

The factor pairs referred to in this paper and their conventional symbols are listed below

A	a	Anthocyanin pigment A factor pair which affects the pigmentation of aleurone, sheaths, leaves, anthers, etc (Emerson, 1918, 1921)
B	b	Sun red plant color (Emerson, 1921)
Bn	bn	Brown aleurone (Kvakan, 1924)
C	c	Color of aleurone (East and Hayes, 1911, Emerson, 1918)
G	g	Golden plant color (Lindstrom, 1918)
J	j	Japonica-striped leaves (Lindstrom, 1918)
Lg	lg	Ligule (Emerson, 1921)
P	p	Color of pericarp (Emerson, 1917)
Pl	pl	Purple plant color (Emerson, 1921)
Ra	ra	Ramosa ears (Gernert, 1912)
Sh	sh	Texture of endosperm (Hutchison, 1922)
Su	su	Texture of endosperm (East and Hayes, 1911)
Tu	tu	Tunicate ears (Eyster, 1922)
Wc	wc	White-capping (Kulkarni, 1926)
Wh	wh	Color of endosperm (White, 1917)
Ws	ws	White sheaths (Kempton, 1921, Clark, 1926)
Wx	wx	Texture of endosperm (Collins, 1909)
Y	y	Color of endosperm (East and Hayes, 1911, Emerson 1921)

LINKAGE RELATIONS OF WHITE-CAPPING

When it was definitely found that the white-capping factor is inherited in a simple Mendelian way and that the white-capping in the various varieties of corn investigated was due to the same factor, it was thought desirable to investigate the relations of this factor to the other factors in different linkage groups of maize

Since white-capping does not show on white seeds and is dominant to yellow seeds, all the testers must have yellow endosperm color

Relation of (Wc) to C, sh, wx group

In order to ascertain the relationship of *Wc* factor to *C* factor, it was crossed with yellow *C* tester The F_1 hybrids thus obtained were crossed with the double recessive (*cY*) Four backcross progenies gave 856 purple and 832 white-capped yellow and yellow seeds (Table VI) The deviation from the expected 1 1 ratio is 12 00 ± 13 85 and is not significant

White-capped yellow was crossed with the pollen of yellow shrunken and the F_1's thus obtained were backcrossed with the double recessive The results of these backcrosses are shown in Table VII Nine backcrosses gave 2567 seeds of parental combinations and 2634 recombinations The deviation from the expected 1 1 ratio is 33 5 ± 24 30 and is not significant This indicates that the factors *Wc* and *sh* are independently inherited

Relation of white-capping (Wc) to R, l, g, pg_1 group

White-capped yellow (*WcY*) was crossed with the pollen from yellow golden (*Yg*) plants and the F_1's were backcrossed with the double recessive (*Yg*) Five backcross progenies gave 247 plants of parental combinations and 231 of recombinations (Table VIII) The deviation from equality of 8 00 ± 7 37 suggests that *Wc* and *g* segregate independently

Relation of white-capping (Wc) to su, Tu group

Crosses were made involving *WcY* and *su Y* The F_1's were then backcrossed with the double recessive (*su Y*) Ten such backcrosses on classification gave 1774 seeds of parental combinations and 1791 seeds of recombinations (Table IX) The deviation from the expected 1 1 ratio is 8 5 ± 20 13 and is not significant This shows that *Wc* and *su* are inherited independently

WcY was crossed with *Tu Y* and the resulting hybrid was backcrossed with the double recessive *tu Y* Four backcross progenies gave 117 plants of parental combinations and 132 of recombinations (Table X) The deviation from the expected 1 1 ratio, 7 5 ± 5 32, indicates that *Wc* and *Tu* are inherited independently

Relation of white-capping (Wc) to Y, Pl, sm group

Plants from white-capped yellow endosperm seeds (*WcY*) were crossed with yellow endosperm brown plants (*a B Pl Y*) The F$_1$ hybrids resulting from this cross were then crossed with the pollen of yellow endosperm dilute sun-red (*A b pl Y*) plants in order to test the linkage of white-capping factor (*Wc*) with *B* and *Pl* factors for plant colors A classification of the plants from these backcrosses is presented in Table XI For *B* factor the plants of these backcrosses gave 368 plants of parental combinations and 373 of recombinations The deviation from equality is 2 5 ± 9 18 and is not significant Classification of plants with respect to *Pl* factor gave 364 plants of parental combinations and 377 of recombinations. The deviation from the expected 1 1 ratio is 6 5 ± 9 18 and is not significant These results show that white-capping (*Wc*) is linked with neither *B* nor *Pl*

Relation of white-capping (Wc) to lg, B, sk, Ts_1, v_4 group

Additional data were obtained regarding the independent inheritance of white-capping factor and *B* group of linked factors *Lg*, which is known to be linked with *B*, was crossed to the white-capped yellow The hybrids were then crossed with the pollen of the double recessive (*Y lg*) A classification of the plants from these backcrosses is given in Table XII Of the 491 plants observed from these backcrosses 258 plants were parental combinations and 233 recombinations. The deviation from equality of 12 5 ± 7 47 suggests independent inheritance of *Wc* and *lg*

Relation of white-capping (Wc) to P, br, f group

In order to test the linkage of *Wc* with *P* factor, *Wcy* was crossed with red-cobbed white yellow endosperm (*P Y*) The F_1 hybrids thus obtained were then crossed with the pollen of white-cobbed yellow (*Y p*) A classification of ears from these backcrosses gave 210 ears of parental combinations and 275 of recombinations (Table XIII) The deviation from the expected 1 1 ratio is 32 5 ± 7 43, which is 4 4 times the probable error Although the deviation is large, it is believed not to be significant because the recombination group is in excess of the parental group This shows that *Wc* and *P* segregate independently

Relation of white-capping (Wc) to A group

White-capped yellow endosperm plants (*Wc Y*) were crossed with brown plants (*a B Pl Y*) The F_1 hybrids were then crossed with the pollen from brown plants (*a B Pl Y*) A classification of plants from ten such backcrosses gave 408 plants of parental combinations and 411 plants of recombinations (Table XIV) The deviation from the calculated 1 1 ratio is 6 5 ± 9 65 This suggests the independent segregation of *Wc* and *A* factors

Relation of white-capping (Wc) to Bn, gl, v_5, Ra group

Plants originating from white-capped yellow seeds (*Wc Y*) were crossed with the pollen from yellow endosperm ramosa (*Y Ra*) plants The F_1 hybrids thus obtained were self-pollinated the next year F_2 progenies of two pedigrees involving the interrelations of these two factors are shown in Table XV White-capped yellow seeds gave 175 normal and 50 ramosa plants. The deviation from the calculated 3 1 ratio was only 6 25 ± 4 38 The yellow seeds gave 60 normal and 20 ramosa plants The deviation in this case was 00 ± 2 61 These results show the free segregation of *Wc* and *Ra*

Miscellaneous linkage tests

White-capped yellow (*WcY*) was crossed from the pollen from white-sheath (*ws*) plants (Kempton, 1921, Clark, 1926) The F_1 hybrids were then backcrossed with the double recessive (*Y ws*)

Four such backcross progenies gave 224 plants of parental combinations and 190 of recombinations (Table XVI) The deviation from equality of 17 00 ± 6 86 suggests that *Wc* and *ws* are not closely linked

Plants originating from white-cap yellow endosperm (*Wc Y*) were crossed with the pollen of yellow japonica (*Y j*) The hybrids thus obtained were backcrossed with the pollen of the double recessive yellow japonica (*Y j*) Only one pedigree was grown, which gave 86 plants of parental combinations and 73 plants of recombinations The deviation from the calculated 1 1 ratio is 6 5 ± 4 25 and is not significant This shows that *Wc* and *j* are inherited independently

SUMMARY

1 White-capping factor (*Wc*) is shown to be dominant to dominant white endosperm (*Wh*) and yellow flint in F_1 and segregates in a mono-hybrid ratio in F_2 in both cases

2 White-capping (*Wc*) of all the varieties investigated is genotypically and phenotypically the same

3 White-capping (*Wc*) is not linked with *C*, *sh*, *wx*, *g*, *su*, *Tu*, *B*, *lg*, *Pl*, *A*, *P*, *Ra*, *ws* and *j*

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TABLE I

PROGENY OF THE SELF-POLLINATED SEEDS OF DOUBLE-CROSSED BURR LEAMING

Pedigree No	Yellow		White (y)
	White-cap Yellow (Wc Y)	Yellow (Y)	
4-4	385	125	166
4-32	207	69	89
4-43	266	81	114
4-45	245	78	110
4-52	231	80	103
4-68	321	101	137
4-45 A	184	61	87
Total	1839	595	806
Calculated 9 7	1822 5	1417 5	
Deviation	16 5 ± 19 02		

TABLE II

PROGENY OF THE SELF-POLLINATED SEEDS OF DOUBLE-CROSSED BURR LEAMING

Pedigree No	White-cap yellow (Wc Y)	Yellow (Y)
4-7	203	72
4-33	249	86
Total	452	158
Calculated 3 1	457 5	152 5
Deviation	5 5 ± 7 21	

TABLE III

F_2 PROGENY OF THE CROSS DUNCAN (*wcY*) × NORTHWESTERN DENT (*WcY*)

Pedigree No	White-cap Yellow (Wc Y)	Yellow (Y)	White (y)
9-4	271	94	105
9-24	321	112	137
9-27	311	110	135
9-34	274	88	110
9-35	381	128	159
9-46	322	106	124
9-47	425	145	175
9-54	396	129	168
9-61	314	107	130
10 1	312	105	120
10-4	295	95	113
10-7	309	101	135
10-10	390	138	173
10-18	315	104	125
10-22	266	89	112
Total	4902	1651	2021
Calculated 9 7	4823 1	3751 3	
Deviation		79 3 ± 30 95	

TABLE IV

F_2 DATA OF THE CROSS WHITE-CAP YELLOW (*Wc Y*) × DOMINANT WHITE ENDOSPERM (*Wh*)

Pedigree No	White-cap yellow (Wc Y)	White (Wh)
385-4	385	104
385-14	241	81
385-15	190	72
387-13	312	124
387-15	392	122
Total	1520	503
Calculated 3 1	1517 25	505 75
Deviation	2 75 ± 13 14	

TABLE V

DATA OF THE CROSS WHITE-CAP YELLOW (*Wc Y*) × YELLOW FLINT (*wc Y*)

Pedigree No	White-cap yellow (Wc Y)	Yellow (Y)
388-10	334	119
388-15	396	136
388-18	376	125
Total	1106	380
Calculated 3 1	1114 5	371 5
Deviation	8 5 ± 11 24	

TABLE VI

PROGENIES OF THE BACKCROSS (*C Wc Y* × *c Y*) × *c Y*

Pedigree No	Purple (C)	Yellow (Y) and white-cap Yellow WcY		
		Yellow and white-cap yellow (c)	White-cap yellow (Wc Y)	Yellow (Y)
35-2 × 77-12	226	202	96	106
35-6 × 77-19	233	232	102	130
35-10 × 77-20	197	192	98	94
35-13 × 77-20	200	206	83	123
Total	856	832	379	453
Calculated 1 1	844	844	416	416
Deviation	12 00 ± 13 85		37 00 ± 9 73	

TABLE VII

PROGENIES OF THE BACKCROSS (*Sh Wc Y* × *sh Y*) × *sh Y*

Pedigree No	Parental combinations		Recombinations	
	Wc Sh	wc sh	Wc sh	wc Sh
30-2 × 77-5	141	152	156	153
30-4 × 77-4	155	125	134	158
30-16 × 77-3	173	174	172	169
30-39 × 77-6	125	106	122	133
30-42 × 77-6	143	147	156	156
30-45 × 77-7	137	130	138	137
30-48 × 77-7	106	116	112	108
30-49 × 77-8	145	147	146	141
30-50 × 77-8	173	172	179	164
Subtotal	1298	1269	1315	1319
Total	2567		2634	
Calculated 1 1	2600 5		2600 5	
Deviation	33 5 ± 24 3			

TABLE VIII

PROGENIES OF THE BACKCROSS (*G Wc Y* × *g Y*) × *g Y*

Pedigree No	Parental combinations		Recombinations	
	Wc G	wc g	Wc g	wc G
27-5 × 87-9	37	40	34	35
27-2 × 87-1	26	23	23	24
27-23 × 87-5	16	24	15	20
27-1 × 87-7	23	17	23	20
27-15 × 87-1	18	23	16	21
Subtotal	120	127	111	120
Total	247		231	
Calculated 1 1	239		239	
Deviation	8 00 ± 7 87			

TABLE IX

Progenies of the Backcross (*Su Wc Y* × *su Y*) × *su Y*

Pedigree No	Parental combinations		Recombinations	
	Wc Su	wc su	Wc su	wc Su
221-1 × 289-3	77	74	65	71
221-27 × 289-23	87	98	99	96
221-4 × 289-3	93	90	92	93
221-29 × 289-1	93	91	95	88
289-23 × 221-6	71	67	66	76
312-11 × 289-23	113	105	107	109
312-10 × 289-23	90	77	98	80
312-12 × 289-2	94	83	85	89
312-15 × 289-14	103	107	108	114
312-17 × 289-12	79	82	83	77
Subtotal	900	874	898	893
Total	1774		1791	
Calculated 1 1	1782 5		1782 5	
Deviation	8 5 ± 20 13			

TABLE X

Progenies of the Backcross (*tu Wc Y* × *Tu Y*) × *tu Y*

Pedigree No	Parental combinations		Recombinations	
	Wc Tu	wc tu	Wc tu	wc Tu
1-6 × 51-4	20	19	30	24
1-34 × 51-6	14	15	15	22
1-30 × 51-3	17	17	16	17
1-24 × 51-12	10	5	3	5
Subtotal	61	56	64	68
Total	117		132	
Calculated 1 1	124 5		124 5	
Deviation	7 5 ± 5 32			

TABLE XI

Progenies of the Backcross ($A\ b\ pl\ Wc\ Y \times a\ B\ Pl\ Y$) × $A\ b\ pl\ Y$

Pedigree No	White-cap yellow (Wc Y)				Yellow (Y)			
	Purple	Sun-red	Dilute purple	Dilute sun-red	Purple	Sun-red	Dilute purple	Dilute sun-red
	WcABPlY	WcABplY	WcAbPlY	WcAbplY	wcABPlY	wcABplY	wcAbPlY	wcAbplY
1-12 × 39-6	24	20	16	17	16	21	20	25
2-23 × 26-17	2	9	2	6	8	6	6	8
1-143 × 26-3	3	7	15	6	7	9	12	10
1-141 × 26-43	13	6	4	12	14	13	5	9
1-142 × 26-43	15	9	7	10	14	11	9	10
1-118 × 39-38	12	16	8	12	11	13	10	7
1-116 × 39-11	7	17	8	16	16	12	13	3
1-132 × 44-11	2	10	8	8	9	14	8	12
1-131 × 44-6	9	3	10	6	3	5	6	11
Total	87	97	78	93	98	104	89	95

TABLE XII

PROGENIES OF THE BACKCROSS (*Lg Wc Y* × *lg Y*) × *lg Y*

Pedigree No	Parental combinations		Recombinations	
	Wc Lg	wc lg	Wc lg	wc Lg
200-36 × A 5072-11	34	23	24	26
200-30 × A 5072-7	29	26	30	23
204-15 × 292-5	56	37	53	33
208-3 × 292-4	25	28	17	27
Subtotal	144	114	124	109
Total	258		233	
Calculated 1 : 1	245.5		245.5	
Deviation	12.5 ± 7.47			

TABLE XIII

PROGENIES OF THE BACKCROSS (*P Wc Y* × *P Y*) × *p Y*

Pedigree No	Parental combinations		Recombinations	
	Wc P	wc p	Wc p	wc P
146-4 × 147-30	23	18	25	26
146-3 × 147-30	27	16	29	39
306-8 × 147-47	21	25	32	39
319-6 × 147-37	32	22	26	26
306-1 × 147-44	18	8	20	13
Subtotal	121	89	132	143
Total	210		275	
Calculated 1 : 1	242.5		242.5	
Deviation	32.5 ± 7.43			

TABLE XIV

Progenies of the Backcross (*A Wc Y* × *a B Pl Y*) × *a B Pl Y*

Pedigree No	Parental combinations		Recombinations	
	Wc A	wc a	Wc a	wc A
26–2 × 91–2	11	13	28	20
26–6 × 91–7	18	21	24	12
26–59 × 91–2	15	9	8	12
26–4 × 91–2	22	21	18	13
39–17 × 91–12	12	25	25	17
39–2 × 91–12	19	26	27	15
36–9 × 91–15	17	28	21	32
39–23 × 91–13	5	22	21	11
43–5 × 91–15	13	16	15	10
44–7 × 91–12	24	17	23	17
44–5 × 91–16	26	23	19	28
Subtotal	182	221	229	187
Total	403		416	
Calculated 1 1	409 5		409 5	
Deviation	6 5 ± 9 65			

TABLE XV

F_2 Progenies of the Cross (*ra Wc Y* × *Ra Y*)

Pedigree No	Number of plants from white-capped seeds		Number of plants from yellow seeds	
	Wc Ra	Wc ra	wc Ra	wc ra
308–1	89	25	27	10
308–2	86	25	34	9
Total	175	50	61	19
Calculated 3 1	168 75	56 25	60	20
Deviation	6 25 ± 4 38		00 ± 2 61	

TABLE XVI

PROGENIES OF THE BACKCROSS (*Ws Wc Y* × *ws Y*) × *ws Y*

Pedigree No	Parental combinations		Recombinations	
	Wc Ws	wc ws	Wc ws	wc Ws
152-7 × 301-10	56	22	18	43
317-1 × 301-14	44	16	6	35
317-9 × 301-14	24	12	10	40
152-21 × 301-5	31	19	9	29
Subtotal	155	69	43	147
Total	224		190	
Calculated 1 1	207		207	
Deviation	17 00 ± 6 86			

THE WATER SUPPLY OF THE EPIDERMIS OF LEAVES *

CARL D LA RUE

WHILE walking through a dry wood on an August day (1929) the writer noticed that the leaves of plants of *Mitchella repens* had a curious appearance The epidermis on the lower side of the leaf appeared to be puffed out and separated from the mesophyll and completely unattached except along the midrib and at the leaf margin A number of plants were examined in which all except the youngest leaves had the lower epidermis and one layer of cells above it separated from the mesophyll The layer immediately adjoining the epidermis was attached to it rather firmly and had thick cellulose walls In the older leaves this layer had no connections with the mesophyll at all

The unusual separation of the epidermis and the layer of cells next to it from the mesophyll raised the question as to how these cells secured a supply of water and also of food It seems that this supply must come from the midrib and from the veins along the leaf margins, since there is no opportunity for a transfer through the mesophyll Presumably, in most leaves the water and the food travel through the cells of the spongy parenchyma by the shortest route to the epidermal cells Thus far the writer has been able to find no discussion in the literature which bears on this point, perhaps because for most leaves the process is obvious But in these leaves the usual channels are cut off It may be that a certain amount of water is secured by the cells in question by condensation from the air, particularly at night when the humidity is high In the case of the leaves described above this seems doubtful because of the dry weather and the drought of the surrounding air In times of more abundant rainfall the condensation may well supply the rather small amount of water which these cells should require It should be remembered that the epidermal cells are rather heavily cutinized on the outside and so give off water to any extent only on the inner surfaces of the cells The layer beneath the epidermis is not cutinized at all and these cells must have a much higher rate of water loss than those of the epidermis It is uncertain whether these cells can secure sufficient water by condensation and by absorption of water vapor to keep them alive in periods of drought That they were alive was shown by the microscopic examination which proved that they were in perfectly normal condition Therefore, it seems reasonable to suppose that water, as well as food, is supplied by transverse conduction from the midrib and from the vascular bundles along the margins of the leaves

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To see whether leaves of other species showed a similar construction of the lower epidermis, examination was made of many plants of the local flora and of exotics in the greenhouses of the University of Michigan Botanical Gardens, in those at Belle Isle, Detroit, and in several belonging to commercial firms None were found that were quite the same, but a few had areas of loose epidermis along the midribs and along the main veins This condition was seen in *Betula alba papyrifera*, *Hieracium venosum*, *Aster laevis* and *Rhus borealis* Leaves of the first three of these species were imbedded and sectioned Study of the sections showed some slender strands of spongy parenchyma between the epidermis and the mesophyll proper, but these were few and in decided contrast to the well-developed connections of the epidermis with the midribs and the veins

Saxifraga sarmentosa was found to have white stripings on the upper surfaces along the veins They are due to the fact that these areas are slightly raised from the underlying palisade cells However, these lie directly above the veins and are not in connection with them, but must get their water supply by transverse flow from the adjoining cells on either side

Kraemer, in his text, *Applied and Economic Botany*, figures a cross-section of a leaf of digitalis which shows a separated or additional layer of epidermis along the midrib This layer is entirely separated from the remainder of the leaf except at its outer edges and bears both glandular and non-glandular hairs on its surface From Kraemer's figure the layer beneath this extra epidermis appears to be exactly like the lower epidermis elsewhere on the leaf If these epidermal cells are cutinized, as they appear to be, this extra layer must secure its water supply by transverse flow from its edges, and in addition to supplying the water lost by transpiration from the surfaces of the cells it must also furnish water to the hairs, glandular and non-glandular

Some evidence of the ability of epidermis to survive without connections with the mesophyll was gained from the burrows of various leaf-miners which eat out the mesophyll, leaving the epidermis intact above and below the burrow The writer recalls a beautiful example of this in a species of Phyllanthus in Sumatra in which the leaf-miner removed practically all the green tissue The main veins were left intact and the miner passed around these at the outer ends, where they were thin enough to allow it to crowd between the vein and the epidermis Nothing was left of the leaf except a shell of epidermis and the most prominent veins, but the leaves did not wither, they remained intact for some time

No such complete mining of leaves has been observed in Michigan, but a number of species of plants show leaf mines of lesser extent and these were studied with some care Extensive mines which isolated either the upper epidermis, the lower epidermis or both upper and lower epidermis, were observed in leaves of *Smilacina racemosa*, *Catalpa bignonioides*, *Lactuca scariola*, *Rumex crispus*, the cultivated columbine and the hollyhock In all these plants the isolated patches of epidermis were intact and appeared to be normal in all respects Leaves of *Quercus alba* were found which had very extensive leaf mines which isolated tracts of epidermis more than an inch square However, the epidermis over such mines did not survive very long, but became dry and withered, although it remained alive for perhaps three weeks

Narrow tunnels made by miners were often observed in leaves of *Populus grandidentata*, *Populus tremuloides* and *Arctostaphylos* The epidermis over these tunnels usually appeared to be alive, although portions were found which were dead Mines of another type were found on *Populus grandidentata* which were much wider than the so-called tunnels Over these the epidermis was alive, or at least it appeared to be alive and normal Portions of leaves with such tunnels were fixed, imbedded and sectioned to determine the real condition of the epidermis It was found that the epidermis above and below the mines was exactly like that on undisturbed portions of the leaf It was interesting to note that the miner seemed to discriminate between different portions of the leaf In many leaves the insect ate only the spongy parenchyma and the lower palisade cells, and left the upper row of palisade cells unharmed In other parts of the burrow all the palisade was eaten and the upper epidermis was left isolated The layer of mesophyll immediately inside the lower epidermis was never eaten This layer consists of one row of cells which have thicker walls than the other cells of the spongy parenchyma and it may be that these are too tough to be relished by the larvae When the lower epidermis is isolated, it is subtended by a second layer of cells, as is the case in Mitchella All the cells in both layers appear to be undisturbed by the removal of the mesophyll inside

On *Aster laevis* a leaf-spot due to an unidentified smut fungus was found in which both the upper and the lower epidermis appeared to be pried loose from the mesophyll On this account the epidermis looked white because of the air extruded, but apparently it remains alive until ruptured by the mass of spores extruded Spots with immature spores were imbedded, sectioned and studied Patches of epidermis of considerable extent were found to be completely separated from the mesophyll by the growth of the fungous tissue and abnormal leaf cells In this leaf there was no layer of mesophyll cells which separated from the other cells of the spongy parenchyma and remained attached to the lower epidermis, as in the other leaves which were sectioned, but the epidermis, both above and below, was separated cleanly from the mesophyll The condition of the separated epidermis was in no visible way different from that of the epidermis of normal parts of the leaf

Paraffin sections across leaf mines in leaves of *Arctostaphylos* *uva-ursi* showed that, though the epidermis over the mines frequently remained alive and unchanged, it sometimes became brown and abnormal in appearance and sometimes died and withered

It is apparent from the examination of various leaves that the epidermis may be able to survive without connection with the mesophyll, either when the separation is natural, as in *Saxifraga sarmentosa* and *Mitchella repens*, or when it is caused by the growth of a fungus or by the burrowing of an insect The last two types of separation might be suspected of causing some injury to the epidermis, but the tissue is capable of surviving that in addition to the cutting of its communications with the mesophyll

A few experiments were made in the attempt to separate the epidermis from the mesophyll in ways other than those offered by the agencies of insects and fungi The first method tried was that of injecting water under the epidermis with a hypodermic needle, so that the epidermis would be lifted and separated by the pressure of the water This was tried on both the upper and the lower epidermis of a number of leaves Most of them were too thin to admit the insertion of the needle, but in other leaves the whole mesophyll became injected without any lifting of the epidermis In a few plants the lower epidermis was lifted successfully and puffed out to such an extent as to leave no doubt that all connections with the spongy parenchyma were broken The species in which this was done were *Aster laevis*, *Hieracium venosum*, *Mitchella repens*, and *Saxifraga sarmentosa* In the first two the whole epidermis was lifted from midrib to margin for one third to one half the length of the leaf In Mitchella the epidermis was lifted over all of one side of the leaf and in Saxifraga the space between two of the principal veins was involved in each injection In a few hours the water disappeared and the swelling caused by it subsided, allowing the epidermis to sink back to its normal position After three weeks the areas which had been injected could be detected still, but no dead cells were visible Examination proved that the epidermis was alive over all the injected areas. Except in the case of *Saxifraga sarmentosa* all the experiments were made on plants living in dry woods The Saxifraga was a potted plant and was kept in the laboratory In none of the plants was the condition an abnormal one, and the epidermis which had been separated from the mesophyll was subjected to the same transpiration rate as that of undisturbed leaves on other plants of the same species

It is possible that, when the epidermis which has been pried loose by water pressure settles back into normal position, it again forms contacts with the spongy mesophyll by which it can secure water This may be doubted because the external appearance of the injected areas is different from that of normal areas and suggests that the separation persists. But in order to be certain about the question another method was used It was found that the epidermis of some leaves could be separated by running a probe between it and the mesophyll A slender glass tube was drawn out to a thin long point The end was then melted to form a small ball which could be pushed along under the epidermis Some practice was needed to develop skill enough to lift an area of epidermis of considerable extent without tearing it at any point It was found that too small a ball at the tip of the probe would tear the epidermis or the parenchyma cells instead of separating them, but too large a ball put too much tension on the epidermis and ruptured it

It proved an easy task to separate the lower epidermis of snapdragon from the mesophyll, but the upper epidermis could not be separated from the palisade In *Saxifraga sarmentosa* both the upper and the lower epidermis could be lifted, though not so easily as the lower epidermis of snapdragon When it was once lifted the epidermis was held in place by sliding under it a piece of glass tubing of small bore and with blunt ends The cut in the epidermis through which the probe and, later, the supporting glass tube were inserted was sealed with vaseline

The epidermis is surprisingly tough especially in the Saxifraga, and could be lifted without much difficulty over leaf areas 20 mm long by 8 mm wide Not many plants were tested as subjects in this experiment, but it is likely that the epidermis may be lifted in a number of others, and it may be that this fact would be useful in some infection studies in which the inoculum could be inserted under the epidermis

Three weeks after this experiment was made on a number of leaves on plants in the laboratory, microscopic examination was made of the epidermis to determine its condition In *Saxifraga sarmentosa* both the upper and the lower epidermis survived the operation, except that in some cases a small spot on top of the supporting glass tube was dead In the snapdragon the epidermis was alive wherever the width of the separated area did not exceed 3 mm, but where the area was 7 or 8 mm wide the central portion was dead though still intact Along each side of the dead strip an area about 2 mm wide was still alive

Although it is certain from the foregoing observations and experiments that fairly extensive areas of epidermis can survive for an indefinite period the separation from the underlying mesophyll, whether this separation is effected naturally or by such rough means as jaws of larvae or by glass probes, it is not sure that the separated cells are not supplied with water by condensation, or by the absorption of water vapor

An attempt was made to isolate the epidermis from water vapor by coating it on the inside with vaseline The lower epidermis on leaves of snapdragon and saxifrage was lifted by a glass probe and then smeared with vaseline on a small pledget of cotton After three weeks the leaves were examined and it was found that the epidermis of the saxifrage was alive and in good condition, except along the cuts made for the insertion of the probe The epidermis of the snapdragon had died, perhaps from the vaseline and rough handling in its application, perhaps from lack of water

On leaves of the saxifrage areas of epidermis were loosened, cut free on three sides, and turned back as a flap The lower surface was then smeared with vaseline and the flap turned back into place In spite of this treatment the cells remained alive and turgid except along the cut edges Of course, the amount of water needed by these cells is not great, since they are cutinized on the outside and coated with vaseline on the inside, but some cuticular transpiration undoubtedly takes place and the only source of water to supply this loss is by lateral transfer through the cells along the uncut side of the flap

A further attempt at isolation of the epidermis was made by injecting melted vaseline with a hypodermic syringe under the epidermis after it had been lifted by a probe In other leaves the epidermis was lifted by pressure of the injected vaseline without preliminary lifting with a probe The experiment was tried on both snapdragon and *Saxifraga sarmentosa*, but in all cases it led to the death of the whole injected area of each leaf

An approach to the problem from another angle was attempted If an area of epidermis could be cut off from communication with the surrounding epidermis, one could determine to what extent transfer of water through the spongy mesophyll and absorption of water vapor are adequate An effort was made to cut through the epidermis on four sides of an area, but though this was tried on several leaves it was not successful Either the epidermis was left uncut in some places or the cuts went deep into the leaves or entirely through them

The evidence that the epidermis, or at least reasonably large areas of it, can survive without connection with the mesophyll is adequate, but that tending to show that it can survive when cut off from the possibility of absorption of water vapor is less satisfactory Probably under normal conditions the water supply of the epidermis is gained by lateral transfer from the veins, by transfer through the spongy parenchyma, and by absorption of water vapor from the air spaces However, when the transpiration is strong the inner surfaces of epidermal cells must lose water to, rather than absorb it from, the air spaces In dry periods the separated epidermis of Mitchella must depend very largely on water supplied by lateral transfer from the veins So far as food is concerned, the epidermis of Mitchella and the areas of epidermis in other leaves which become isolated by insect burrows or fungous attack must secure the amount needed by lateral transfer alone

SUMMARY

In mature leaves of *Mitchella repens* the lower epidermis and one layer of cells inside it become separated from the mesophyll and remain attached only at the midribs and margins In this condition the cells remain alive and normal

In a number of species areas of upper and lower epidermis remain alive after separation from the mesophyll by tunnels of leaf-miners, or by masses of fungous spores

In several species the epidermis which has been separated from the mesophyll by injection of water remains alive and uninjured

The epidermis of some plants will remain alive after it has been lifted by a probe and kept separated by a piece of glass tubing In one plant it survived after it has been coated on the inside with vaseline so that absorption of water vapor is impossible

It is possible for the epidermis of the leaves of a number of plants to secure an adequate supply of food and water without any connections with the mesophyll

UNIVERSITY OF MICHIGAN

A STUDY OF *GLONIUM PARVULUM* IN CULTURE *

MARION L LOHMAN

IN 1874 Gerard (4) described a hysteriaceous fungus collected on Alnus as *Hysterium* (*Glonium*) *parvulum* The species was transferred to the genus Glonium by Saccardo (*Syll* , 2 735 1883) and listed as *G parvulum* (Ger) Sacc Of the Glonia described from North American material on woods of deciduous species, this species and *G medium* (Cooke) Sacc have densely gregarious hysterothecia less than 1 mm in length and spores as short as 6 to 8 microns In Saccardo the two are separable only on spore measurements, but, as Ellis pointed out (*North American Pyrenomycetes*, p 682), these are incorrectly given for the former species Since Ellis examined authentic material of Gerard's species and material of *G medium* collected by Ravenel and suggested no affinities here, the two were distinct species to him With his descriptions, however, they can be distinguished only through the more flattened hysterothecia of *G parvulum* and the fact that a blackening of the wood or the presence of a black crust is not mentioned in the case of *G medium* My studies lead me to believe that those characters can hardly be relied upon as specific, and, furthermore, the *G parvulum* distributed by Ellis (*North American Fungi*, p 153) shows very little of the blackened crust mentioned in his description Since my collections from Michigan show this condition and otherwise agree with the *G parvulum* (Ger) distributed by Ellis, I do not hesitate in referring my material to that species

The genus Glonium was established by Mühlenberg in 1813 (*Cat Pl Am Septentr* , p 101) with *G stellatum* as the type species

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* Paper from the Department of Botany of the University of Michigan, No 331

In this species the hysterothecia are decidedly branched and are seated upon a thick byssoid subiculum. In 1918 von Höhnel (6) erected the subgenus Psiloglonium for species without a subiculum, and recently Petrak (13) has given Psiloglonium generic rank (with *P lineare* (Fr) Petr as the type) and is publishing new species under this name

The recent changes in the taxonomy of the Hysteriales, especially by von Höhnel (6), are important for an appreciation of the lack of culture studies in the truly hysteriaceous fungi If one accepts the ideas of von Höhnel in the taxonomy of these fungi and regards the genus Hysterium as typical, then the only culture studies that have been made on these forms are those of Brefeld (3) with "*Glonium lineare* (Fr), *Hysterium pulicare* (Pers), *Hysterographium biforme* (Fr), *Lophium mytilinum* (Pers) *Hysterographium Fraxini* (Pers) " De Bary, Haak, Hartig and von Tubeuf studied pathogenic species which were at that time referred largely to the genus Hysterium, but these are now known as Hypodermataceae, and, if one is influenced by the systematic studies of von Höhnel, they should no longer be considered hysteriaceous fungi For an insight into the taxonomy of the Hysteriales I refer the reader to the excellent compilation of the literature by Bisby (2)

DISTRIBUTION OF *Glonium parvulum* AND DESCRIPTION OF THE ASCIGEROUS STAGE

In view of the fact that we have had no critical study and compilation of the hysteriaceous fungi since the appearance of *North American Pyrenomycetes* by Ellis and Everhart, one can ascertain the distribution of these species only through the ascomycetous lists of various local floras scattered throughout the literature of the last forty years Seaver reports *G parvulum* (Ger) Sacc for North Dakota (16) and Iowa (17) I have several collections on Ulmus from Ingham County, Michigan, a collection on Juglans from Ann Arbor, one collection on Quercus and one on Ulmus from Darke County, Ohio, a collection on Quercus from Randolph County, Indiana, and a collection on Salix from

Montgomery County, Ohio Fink collected extensively in Indiana and Ohio and published from time to time on the ascomycetous flora, but he did not report this species It may be among his more recent collections of Hysteriaceae, however, since they remain unstudied Van Hook does not report it in his lists of Indiana fungi This is the first report of the species for Michigan

Hysterothecia in well-matured material of *G parvulum* are densely gregarious in more or less parallel series and thus form black areas which are readily noticeable to the naked eye (Pl XXIX) The degree of superficiality, blackening of the wood in intermediate areas, and the presence of a black crust are variable characters and apparently depend upon the nature of the substratum and rate of growth The thin black crust is the result of superficial mycelial growth and is more pronounced on transverse surfaces of decaying wood or on the patches of medullary rays which are exposed in radial splits Here the hysterothecia are superficial from the first In still firm and recently decorticated wood there is only a slight blackening of tangential surfaces, where fruiting has occurred on much weathered wood this is not apparent On tangential surfaces the hysterothecia are formed just beneath and at the level of the wood, and later become erumpent-superficial Here, to a large extent, they are seated at the ends of medullary rays (Pl XXX, Fig 2)

The hysterothecia are carbonaceous, black, rugose-punctate, oblong to broadly elliptic, at first somewhat crested above, but becoming broadly flattened or occasionally slightly rounded at the obtuse ends, and measure 250–400 (500) × 150–200 microns The disk is punctate with a central longitudinal furrow and often there are two to four minute striae parallel to the line of dehiscence Studies on sectioned hysterothecia show the lips to be acutely rounded and the central furrow prominent before asci are apparent in the developing hymenium The asci (Pl XXX, Fig 3) are cylindric, short stipitate, 40–55 (60) × 4–5 microns, 8-spored, with simple, slender, filiform paraphyses, curved and interwoven above The spores are oblong, hyaline, obliquely or irregularly uniseriate to subbiseriate, nearly equally two-celled or with the upper cell somewhat broader, rounded at the ends or occasionally with the lower cell subobtuse, decidedly constricted at the septum, and measure 6–8 × 2 5–3 microns.

CULTURE STUDIES

On October 14, 1928, a collection of this species was obtained from splints of a much weathered log of Ulmus in a swampy wood southeast of Stockbridge, Michigan. This collection shows well the blackening of the wood about the patches of gregarious hysterothecia (Pl XXIX) Culture work in other species prevented an immediate attempt to isolate this fungus, but on February 21, 1929, a spore suspension was sprayed on plates of nutrient agar [1] and the spores germinated at room temperature within twenty-four hours From these sprays single spore and single ascus cultures were obtained on February 23

Isolation in pure culture is not difficult in this group, if a few simple precautions are observed Under a low magnification hysterothecia are removed from the wood with sufficient care to keep the wall from being broken These are plunged for an instant into 95 per cent alcohol and then washed in a 1 1000 solution of bichloride of mercury for thirty seconds to one minute They are then rinsed in several changes of sterile distilled water and soaked from twelve to twenty-four hours, when they are transferred to a flamed glass slide and again rinsed to replace the water in which they have been soaking A spore suspension is made by crushing the hysterothecia and washing the hymenial mass into sufficient sterile distilled water to give the desired dilution for spraying

On February 23, 1929, spore suspensions of several species of the Hysteriaceae were sprayed upon plates of an oak-chip infusion agar [2] in a preliminary study These plates and the previous sprays on the synthetic agar were placed in bright light at room temperature, as the work of Leonian (11) had demonstrated that these conditions, in general, are optimum for the development of imperfect stages In the sprays of *Glonium parvulum* a pycnidial development was observed in ten days on the oak-chip infusion agar, which was somewhat less favorable for mycelial development than the synthetic agar By the end of the second week pycnidial development was apparent in the sprays on the latter medium It was then realised that in this species one is dealing with a fungus which will produce an imperfect stage under ordinary culture conditions, and that for more critical work it was necessary only to check the pycnidial development with single spore cultures The details of pycnidial development were determined from more recent culture work and are described later

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[1] Kauffman's synthetic agar To the liter maltose 5 0 gr, peptone 0 1 gr, $MgSO_4$ 0 5 gr, KH_2PO_4 0 25 gr, $Ca(NO_3)_2$ 0 1 gr and agar 15 gr Professor Kauffman has found this to be a very satisfactory medium for general culture work in mycology

[2] Boiled oak chips 8 gr, xylose 5 gr and agar 15 gr The oak-chip solution made up to 1 liter

Ascospore germination

Spores of this species germinate in from twelve to twenty-four hours at 20–25° C, whether on plates of the synthetic agar, in the nutrient solution of the same or in distilled water There is very little swelling of the spore, since germinating spores average 8 5 × 3 5 microns and spores that have not been soaked average 8 × 3 microns Either cell of a spore may be first to put out a germ tube, which is terminal, but ordinarily both cells germinate at the same time (Pl. XXX, Figs 4–5) In several germinating spores, which were unequally two-celled, a second and lateral tube was observed in the upper and larger cell Germ tubes are hyaline, average 2 microns in diameter with no marked constriction at the spore wall, and develop within twenty-four hours either into three- to five-septate hyphae of uniform diameter, 40 to 60 microns in length (becoming branched on nutrient agar plates), or into shorter, closely septate, constricted hyphae with the spherical, basal cells nearly equal to those of the germinating spore The latter is the usual condition on the synthetic agar plates or in the corresponding nutrient solution This formation of spherical cells does not continue, and the subsequent growth is of uniform hyphae, 2–2 5 microns in diameter, with cells 10 to 15 microns in length

In this species individual spores on plates of nutrient agar germinate as readily as spores retained within the ascus.

Cultures on the sucrose-oatmeal medium [3]

On March 24, 1929, transfers from single spore and single ascus stock cultures [4] were made to sucrose-oatmeal slants in large test tubes (4 cm in diameter) One set of subcultures was placed in the light at room temperature and the other set returned to the cold room (0–4° C) after twenty-four hours, where they were subject to similar light conditions

In the light at room temperature — Young mycelial growth is whitish at first, but in a few days becomes pinkish and then "spinel red" to "hellebore red" (R) Growth is rapid but not uniform and cultures at five or six weeks show an irregular margin and a variably erumpent surface mat 2–5 mm deep This condition of growth produces an array of colors, including in addition to those noted above, "vinaceous" or "pinkish cinnamon," "vinaceous fawn" and "avellaneous" Cultures at six to ten weeks present a "purplish-vinaceous" or "purple-drab" discoloration of the medium, but this soon fades to brownish and the cultures themselves no longer show the brighter colors By this time such cultures have completely covered the free surface of the medium (a 10 cm slant, 4 cm in greatest diameter)

In these cultures pycnidia did not appear until after the eighth week, but they were abundant after the tenth week, especially in the single spore cultures By the sixth month they were extremely abundant on older portions of both single spore and single ascus cultures

In the light at 0–4° C — The colors noted above are more persistent at these low temperatures Growth is extremely slow and cultures at ten months average 3 cm in diameter These cultures present the same irregular margin and variably erumpent surface A faint pink discoloration of the medium developed during the fourth month, but this was soon lost in the gradual browning of the oatmeal medium

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[3] To the liter ground oatmeal 60 gr, sucrose 40 gr and agar 15 gr This medium has been used for all stock cultures

[4] In these cultures isolations were made on February 28 and kept in the light at room temperature, transfers were made to the stock medium on March 1, and stock cultures were placed in the cold room the following day All stock cultures mentioned in the work were subject to a similar succession of physical factors.

Pycnidia appeared sparingly in older portions of single spore cultures at six months, and later in single ascus cultures, but they never became abundant in these cultures

For a time the purity of all cultures was questioned on account of the habit of growth and array of colors produced As a check on the stock cultures used, spore sprays were made on December 11, 1929, from different material in this same collection of *G parvulum* A number of single spore and single ascus isolations were made and further studies verified the culture characters noted above A second series of stock cultures was obtained from these isolations

Cultures on Leonian agar[5]

On January 8, 1930, transfers were made to Leonian agar slants from the second series of stock cultures One set of subcultures was left on the laboratory table, where they obtained full light from a north window a second set was placed in the light at 10° C , and the third set was kept in a dark closet at the temperature of the room[6]

In the light at room temperature — Growth is slower on this medium than on the sucrose-oatmeal Vegetative mycelium is mainly confined to the medium and the brighter colors are obscured by a brownish-black, dense, hyphal layer which forms at the surface of the medium There is a rather persistent pink coloration of the medium

Pycnidial development was apparent by the end of the first week and in another week pycnidia were exuding conidial masses

In the light at 10° C — These cultures differed from those of the higher temperatures in that growth was still slower and in that a condition of pycnidial development comparable to that noted above was not attained until the fourth week

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[5] To the liter KH_2PO_4 1 25 gr , $MgSO_4$ 0 625 gr , maltose 6 25 gr malt extract 6 25 gr and agar 15 gr

[6] The cultures of this species were only a part of an experiment to determine the value of the Leonian medium for pycnidial formation in a number of species of the Hysteriaceae

In the dark at room temperature — The cultures were not observed until pycnidia were well developed in the cultures in the light at 10° C Upon examination they showed the same condition of pycnidial development as the cultures in the light at room temperature The medium was colored a deep brown

The observations indicate that the Leonian agar is a favorable medium for the production of a pycnidial stage in this species

Growth at higher temperatures

On January 15 transfers were made from the second series of stock cultures to Leonian and sucrose-oatmeal slants, and after twenty-four hours the subcultures were incubated at 28–30° C, with the same relative moisture conditions as in the previous studies By the sixth week no pycnidia had been formed and vegetative development consisted of a scant, white, aërial mycelium on the surface of the original transfer, although a few cultures showed in addition a marginal growth of several millimeters Only one culture in the lot revealed no development at all

Pycnidial development

This study is based largely upon cultures from undisturbed germinating ascospores on plates of synthetic agar kept in the light at room temperature The mycelium from a single spore is apparent to the naked eye on the third or fourth day and one-week-old cultures are 1 5–2 mm in diameter with a bright reddish central area This central portion soon becomes brownish and enlarges by putting out three to eight or ten radiating arms The pycnidia develop progressively outward within this stellate, brown, hyphal mat (Pl XXXI, Figs 1, 4) As they mature in the central portion, the dense hyphal mat gradually enlarges outward between the arms, and by the fourth or fifth week the radiating structure is not so apparent and cultures are 5–8 mm in diameter, with a black, central, pycnidial area 1 5–3 mm in diameter The border of pinkish vegetative hyphae develops little after this and fades to a yellowish brown

The hyphal mat, within which the primordia develop and upon which the mature pycnidia are seated, shows in section (Pl XXXI, Fig 4) as a thin surface layer of loose, branched, thick and rough-walled, brown, aërial hyphae arising from the thicker and more dense intermediate layer which is developed at the surface of the medium This dark intermediate layer is 10–20 microns in depth about the pycnidial primordia and averages 50 microns in depth where the mature pycnidia are seated The pycnidial primordia are bright red under the microscope, as are the hyphae surrounding them In culture much of this color is concealed by the brownish aërial hyphae The much-branched and anastomosing hyphae of the intermediate layer are closely septate and average 3 microns in diameter This layer forms at the level of, and just within, the surface of the medium It probably corresponds to the black crust occasionally formed on the wood in connection with the perfect stage The substratal hyphae are hyaline, closely septate, branched but loosely interwoven, and penetrate the medium to a depth of 4 mm The three layers of hyphae here referred to are apparently the same as those mentioned by Archer (1, p 7) in his cultural studies of the Sphaeropsidales

Studies based upon free-hand sections and prepared slides indicate that the young pycnidia (as large as 50 70 microns in diameter) are parenchymatic throughout, with a central portion of hyaline, thin-walled cells, and an outer region of cells with thicker brown walls The outermost hyphal cells become opaque as the pycnidium matures In maturing pycnidia, still immersed or somewhat erumpent, the central region is transformed into a cavity of conidial production transversed by sparse, irregular, septate hyphae As the cavity enlarges, these transversing hyphae are no longer discernible and spore production is confined to an even conidiophore layer lining the basal and lateral walls of the pycnidium This condition is attained before there is a suggestion of beak formation (Pl XXXI, Fig 4) As spore production continues, the cavity enlarges upward, following the apical hyphal growth, which develops a short, thick, ostiolate neck (Pl XXXI, Fig 6) by the third or fourth week

Pycnidia exuding conidial masses measure 150–200 microns in diameter, 225–260 microns in height, and have necks 40–60 microns in diameter The length of the neck is variable and depends upon the moisture condition of the culture In the average pycnidium in undisturbed ascospore cultures it is 35–45 microns, in pycnidia from mycelial transfers to oatmeal and Leonian media and in those obtained on oak-chips and oak-infusion agar, necks as long as 155 microns have been observed (Pl XXXI, Fig 2) Pycnidia obtained from single conidium cultures were merely conic-ostiolate Mature pycnidia are black and smooth, more or less irregularly stellately clustered, and in the central, more crowded portion of the cluster the necks are usually somewhat divergent

The pycnidial walls are parenchymatic and they measure (12) 15–25 microns in thickness at the level of the fungus layer upon which the pycnidia are seated The wall of the neck averages 10 microns in thickness and is made up of four to six layers of tightly compacted, brown-walled cells which become opaque in the outermost layers The conidia (Pl XXXI, Figs 5, 7) are hyaline, ovate or inequilateral, 2 × 1 5 microns, and are borne singly on the tips of slender, clavate conidiophores measuring 6–9 × 1 5–2 microns They germinate by one or several germ tubes which are closely septate and soon branch (Pl XXXI, Figs 8–10) The germinating conidia swell to more than twice their initial volume, measuring 3 7–4.5 × 2 5–3 microns Pycnidia exuding conidial masses were obtained within ten days in single conidium cultures on the synthetic agar

TAXONOMIC POSITION OF THE PYCNIDIAL STAGE

The taxonomic characters revealed in the foregoing description of pycnidial development refer the imperfect stage to the Sphaerioideae–Hyalosporae of the Saccardo system (*Syll Fung*, III) It is certainly not stromatic in the sense of Saccardo and therefore belongs to the form-genus Sphaeronaema One might ask, "Is this not an Aposphaeria which has developed a subulate beak in culture?" Aposphaeriae, however, have far more delicate pycnidia and the culture work of Archer (1) with the form-genera Micropera and Naemosphaeria indicates that pycnidia which are beaked in nature do not ordinarily form well-developed beaks in culture

The descriptions in Saccardo are not adequate for comparison The pycnidial stage described here might be *Sphaeronaema procumbens* Sacc , *S cylindricum* (Tode) Fr , *S conicum* (Tode) Fr or *S infuscans* E & E Lack of space prevents a discussion of the present status of these particular forms Considering the treatment given them by Jaczewski, Diedicke and von Höhnel, only *S procumbens* needs further attention, before I dwell upon this it is desirable briefly to survey the status of the form-genus Sphaeronaema

Fries established the genus Sphaeronaema in 1815 (*Observ Myc*, I, p 187), although the usual reference given is to a second publication in 1823 (*Syst Myc*, II, p 535), where *S subulatum* (Tode) stands first In a much later publication (*Summ Veg Scand*, II, p 400 1849) three subgenera were used and here another species stands first in the *Species genuinae* The two important criteria for Fries were the vertically elongate beak and the collection of spores in a mucous mass at the apex Saccardo (*Syll Fung*, III) was the first to suggest the weakness of the second character His system of classification forced a separation of species between the Nectrioideae and Sphaerioideae groups and he retained Sphaeronaema in the Sphaerioideae–Hyalosporae In 1898, Jaczewski (9) revised the genus as established by Fries, with particular reference to the treatment given to it by Saccardo Jaczewski held the beaked or cylindric condition to be of greatest importance and thus readmitted fleshy and carbonaceous forms of various conidial types He was the first to distinguish between parenchymatous and prosenchymatous structures in these forms This distinction Diedicke accepted (*Kryptogamenflora d Mark Brand*, IX, p 286 1915), but in regard to the spore form he retained the genus in the sense of Saccardo

In 1915 von Höhnel (5) indicated needed revisions in this genus and in 1918 he (7) accepted *S subulatum* (Tode) Fr as the type species, and retained Sphaeronaema as a monotypic genus in his Nectrioideae In 1918 he offered (*l c*) valuable criticisms on fourteen other species and indicated the heterogeneity of the genus as used by Saccardo Petrak and Sydow (15) soon pointed out the difficulties involved in accepting von Höhnel's reduction of the Friesian genus To understand von Höhnel's treatment of the other forms in the genus it is necessary to examine his new system of the *Fungi Imperfecti*, a posthumous publication (8) in 1923

In this sytem my pycnidial stage would fall in the Sphaerioideae–Ostiolatae of his Pycnidiaceen, along with two closely related genera, Pleuronaema v H and Ceratophoma v H The latter was erected (7, p 276) to include *S rostratum* Fuckel, a form which differs widely from my pycnidial stage in the nature of the parenchyma cells of the wall and in the conidia, which are elongate-elliptic and measure 2 5–4 5 × 2 microns Pleuronaema v H has *P procumbens* (Fuckel) as the type (*l c*, p 256), and is characterized by allantoid, acrogenetic and pleurogenetic conidia Von Höhnel based his description on material which he believed to be *S procumbens* (Fuckel) Sacc , a European species that had been collected several times on Quercus In the light of his description my pycnidial stage agrees sufficiently in habit, macroscopic appearance and the parenchymatous nature of the wall It differs in that the conidia are smaller, ovate or inequilateral, and primarily in that they are produced singly at the ends of simple conidiophores To follow von Höhnel's system in this case would necessitate the erection of a new form-genus[7]

The discussion here does not do justice to the hopeless condition in the taxonomy of imperfect fructifications of the Sphaeronaema type Real difficulties arise in any manner of presentation of an imperfect stage of this type However, since the pycnidial stage here described is definitely established as an expression in the life-history of *Glonium parvulum*, it seems desirable to present it as

Glonium (Sphaeronaema) parvulum, status novus

> Pycnidia superficial, single or clustered, subulate beaked and ostiolate, smooth, black and carbonaceous, developing from individual primordia within a thin layer of brown, thick-walled, closely septate, branched and anastomosing hyphae, parenchymatous throughout from the first, soon erumpent from the hyphal layer and then each with a developing conidial cavity and ostiolate beak, at maturity 150 to 200 microns

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[7] The new system of von Höhnel is open to several important criticisms which cannot be discussed here Recently Petrak (14) has offered a criticism, but it has little to do with evidence accumulating from cultural studies

in diameter, 225 to 260 microns in height including the beak, the latter 40–125 (155) × 40–60 microns, walls complete, thick, firm, opaque on periphery, brownish inward and at the base, (12) 15 to 25 microns thick, somewhat thinner apically in the beak, small-celled parenchymatous throughout, averaging five to six layers of opaque to brownish cells and several layers of hyaline cells, the innermost layer of hyaline cells giving rise to conidiophores in its basal and lateral portions, conidiophores clavate, 6–9 × 1 5–2 microns, simple though often appearing in tufted clusters of from three to five, conidia acrogenetic, hyaline, ovate to inequilateral or elliptic-oblong and then slightly allantoid, 2 × 1 5 microns, exuded from the beak in dull white masses 200 to 250 microns in diameter, the masses becoming grayish with age

This pycnidial stage is near the Pleuronaema type of the von Höhnel system and differs from it in the thinner pycnidial wall, in the smaller and not definitely allantoid conidia, and primarily in that the conidia are not pleurogenetic as well as acrogenetic The diagnosis is based upon development from single ascospores on various culture media and upon oak chips on the surface of an oak-infusion medium The stage name *Glonium* (*Sphaeronaema*) *parvulum* is suggested as an expedient in comparing this stage with other Sphaeronaemata

Associated perfect stages of Sphaeronaemata and discussion

The association of imperfect stages of the Sphaeronaema type with perfect stages of ascomycetes has been based only upon observation, either in the field or in the herbarium Rostrup (12, p 425) listed eighteen species of Sphaeronaema with their associated perfect stages The latter are represented by Ceratostomella, Dothiora, Dermatea and Tympania. When the list of eighteen species is reduced in the light of von Höhnel's studies (by synonymy and the rejection of species which exist only in name), and when the remaining species are classified as prosenchymatous or parenchymatous (distinct structural types), we find only Sphaeronaemata of the former group corresponding to the discomycetous genera, Dermatea and Tympanis In the parenchymatous group three species remain *S procumbens*, corresponding to *Ceratostomella procumbens*, and *S Fuckelianum* and *rhamni*, corresponding to species of Dothiora

The recent culture studies of Melin (10), in collaboration with others, make the Ceratostomella association appear doubtful Melin obtained a number of species of Ceratostomella in pure culture and Lagerberg referred the conidial stages to the Hyphomycetes as Cladosporium and Cephalosporium types

With an imperfect stage of the parenchymatous Sphaeronaema type established in the life-history of a Glonium species, the puzzle of the phylogeny of hysteriaceous fungi will be more difficult than it has been in the past if a similar connection is established for the species of the dothideaceous genus, Dothiora Even the development of the hysterothecial wall in this species of Glonium suggests that it might be stromatic (with "stroma" meaning any compact vegetative growth not resulting from a sexual stimulus [6]) with the ascigerous cavity developed as in the Dothideales There is obviously a great need for critical studies on hysterothecial development and for further cultural life-history studies, particularly in the genus Glonium Furthermore, no imperfect stage connections occur in the literature on the species of this genus

SUMMARY

1 *Glonium parvulum* (Ger) Sacc can readily be obtained in pure culture from germinating ascospores and under ordinary culture conditions produces a pycnidial stage of the Sphaeronaema type

2 Sucrose-oatmeal agar is a favorable medium for luxuriant mycelial growth, especially at 20–25° C

3 The optimum conditions for pycnidial production in culture are approached when the fungus is grown on either the synthetic medium (Kauffman's synthetic medium, see note 1) or the Leonian medium, in the light at room temperature

4 Pycnidia were obtained from single ascospore cultures and the conidia were germinated. Cultures from germinating conidia produced pycnidia within ten days

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[6] Accepting the definition of Wehmeyer (18, p 579) since it appears extremely usable for the ascomycetes.

5 This pycnidial stage of *G parvulum* established by single ascospore cultures is described in detail to supplement our knowledge of the species The stage name *Sphaeronaema parvulum* is suggested

This study was made in the Department of Botany of the University of Michigan, under direction of Professor C H Kauffman Acknowledgments are due to Dr L E Wehmeyer for a critical reading of the manuscript, and to Mr A H Smith for the photographs of Plate XXIX

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PLATE XXXI

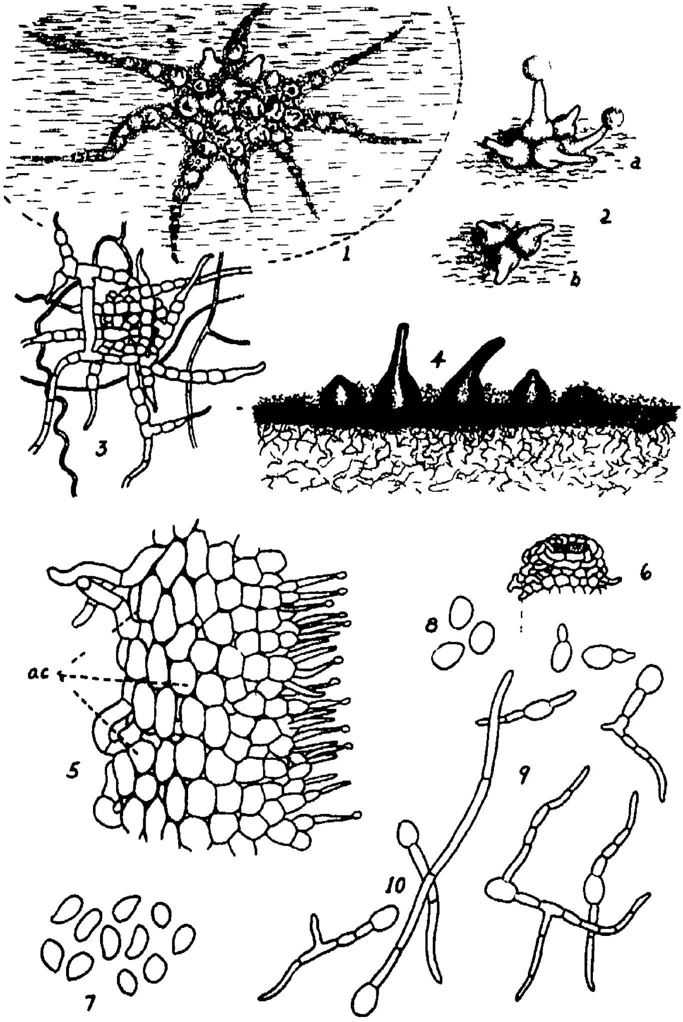
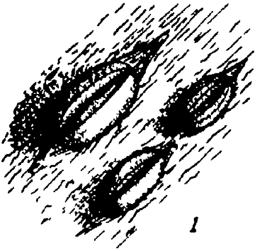


PLATE XXX



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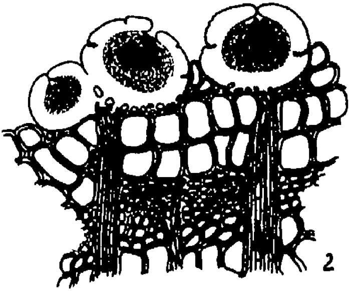

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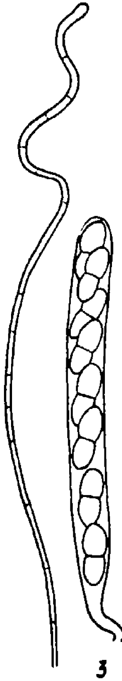

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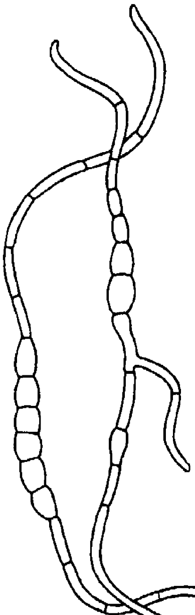

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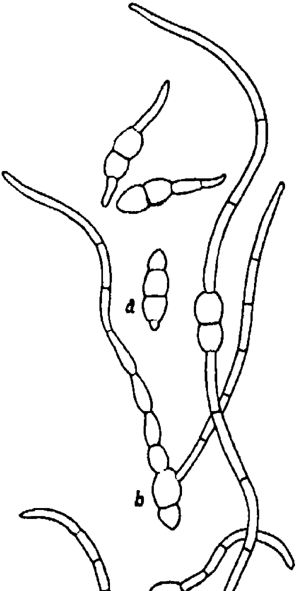

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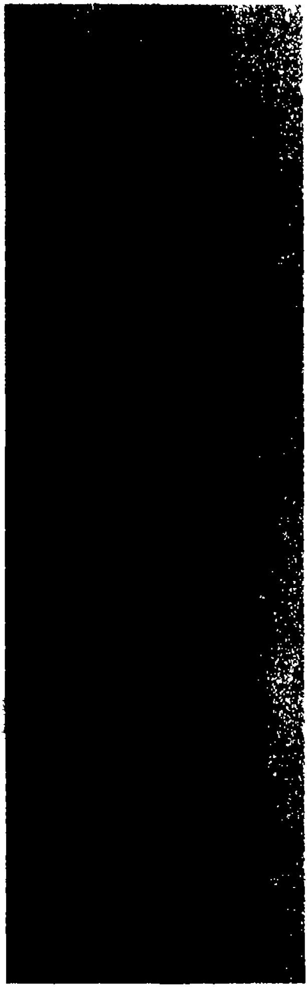
PLATE XXIX



EXPLANATION OF PLATES XXIX–XXXI

PLATE XXIX

Glonium parvulum (Ger) Sacc

Fig 1 Gregarious habit of hysterothecia, twice natural size This material was collected on a weathered log of Ulmus.

Fig 2 Single ascospore culture on sucrose-oatmeal agar, 11 months at 0–4° C , natural size

PLATE XXX

Glonium parvulum (Ger) Sacc

Fig 1 Hysterothecia, × 30

Fig 2 Position and structure of hysterothecia on tangential surface of wood They are ordinarily seated at the ends of medullary rays

Fig 3 Hymenial elements The spores are irregularly uniseriate or subbiseriate

Fig 4. Two germinating ascospores on nutrient agar

Fig. 5 Stages in spore germination in distilled water, *a* and *b* are uncommon

PLATE XXXI

Glonium parvulum (Ger) Sacc , status novus

Fig 1 Habit of pycnidia in undisturbed single ascospore culture on synthetic agar The dotted arc represents the margin of vegetative mycelium

Fig 2 Mature pycnidia, × 50, *a*, on oak infusion agar, *b*, on oak chip with thin agar film.

Fig. 3. Pycnidial primordium

Fig 4. Section study of culture as shown in Figure 1 The dotted line represents the surface of the medium Note the thin layer of aërial hyphae, the dense intermediate layer bearing pycnidia, and the loose substratal hyphae

Fig. 5 Vertical section of lateral wall showing conidiophore types and parenchymatous nature of wall, *a c* , region of opaque cells

Fig 6 Apex of beak showing ostiolate character

Fig. 7 Conidia as seen in water mount

Fig 8. Conidia which did not germinate within twenty-four hours in nutrient solution. Most of the conidia germinated.

Fig. 9 Conidia at various stages of germination in nutrient solution

Fig 10. Germinating conidia on nutrient agar plate.

DETERMINING THE IDENTITY OF MYCORRHIZA-FORMING FUNGI *

RICHARD E McARDLE

THE two methods which have been used by recent workers to determine whether a certain fungus species is a mycorrhiza-former are (1) to produce mycorrhiza in pure culture by inoculating the roots of seedlings with fungus mycelium, and (2) to trace strands of mycelium from a fungus fruit-body to a mycorrhizal root, or, more commonly, to find a fruit-body directly attached to a rootlet The first method, which represents the experimental attack, will not be discussed here This paper is concerned with the second method, which offers an opportunity for immediate identification in the field without the necessity for experimental work lasting several months

It is a difficult, often an impossible, task to trace single strands of hyphae from the fruit-body to a mycorrhizal root Rhizomorphs, or aggregations of fungal hyphae, are somewhat less difficult to trace, especially if the mycelium is colored Finally, fruit-bodies often may be found attached directly to the rootlets When the connection between fruit-body and rootlet could be established in one or another of these ways, it has been customary to consider the fungus a mycorrhiza-former

Perhaps because the circumstantial evidence seemed so conclusive, no investigator has verified the connection by microscopic examination Without microscopic evidence it is obvious that there can be no assurance that the mycelium followed to the root, or that the mycelium forming the fruit-body likewise is responsible for the formation of the mycorrhiza It was the purpose of the investigation here described to test the accuracy of this method of determining the identity of mycorrhiza-forming fungi

During the past three years the writer has conducted extensive

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* Paper from the Department of Botany of the University of Michigan No 334

investigations of mycorrhizal conditions in the coniferous plantations on the Saginaw Forest of the University of Michigan School of Forestry and Conservation Evidence of a circumstantial character was obtained that the fruit-bodies of certain fungi typically occur in apparent contact with the young roots of trees For example, in one of the plantations of white pine the fruit-bodies of *Clitocybe rivulosa* Fr var *angustifolia* Kauff usually occur in "fairy rings" around the trees These rings are especially noticeable in the thinned portions of the stand An attempt was made, by placing stakes, to determine whether the rings of fruit-bodies occurred successively farther outward from the trees at their centers A progressive movement of this sort, year after year, would argue that a definite relation existed between the fruit-bodies and the rootlets, since the young roots capable of forming mycorrhiza yearly advance outward from the trunk of the tree So many rings overlapped that no definite conclusions could be drawn from these observations In the plantations of Norway spruce the fruit-bodies occurred along the roots rather than at the ends Frequently a dozen or more fruit-bodies were found along a three-foot section of spruce root

In these plantations many fruit-bodies were in actual contact with roots, others were directly over large clusters of mycorrhizas and separated from them by only a centimeter or so In the following list are given the names of the species which careful and repeated examination disclosed to be nearly always in close contact with tree roots in the white pine and Norway spruce plantations

In spruce plantation

Amanita muscaria Fr
Cortinarius cinnamomeus Fr
Calvatia saccata (Vahl.) Fr
Cortinarius argentatus Fr
Inocybe eutheloides Pk
Boletus piperatus Bull
Lepiota naucina Fr
Lycoperdon gemmatum Batsch
Lycoperdon pulcherrimum B & C
Clitocybe distreta Fr
Clitocybe rivulosa Fr var angustifolia Kauff
Tricholoma personatum Fr

In white pine plantation

Calvatia saccata (Vahl) Fr
Inocybe eutheloides Pk
Lycoperdon gemmatum Batsch
Collybia butryaceae Fr
Clitocybe diatreta Fr
Clitocybe rivulosa Fr var angustifolia Kauff
Cortinarius sp [1]

Of these species, *Amanita muscaria* has been reported by Melin (5) as forming mycorrhiza on Betula, Larix, *Pinus sylvestris* and *Picea excelsa*, *Cortinarius cinnamomeus* has been reported by Masui (4) as having a similar effect on *Pinus densiflora* and *Populus tremula* var *villosa* The rest, so far as is known, are mentioned for the first time in this connection

The circumstantial evidence obtained in field examinations indicated the existence of an apparently very intimate association between fungus fruit-bodies and tree roots Yet the question still remained Was one justified in assuming on the basis of circumstantial evidence that these fungus species actually were in contact with the *interior* of the roots? In an attempt to check this evidence thirty-four fruit-bodies were obtained which had tree rootlets attached Collections were made in both the white pine and Norway spruce plantations and the fungus species represented were *Lycoperdon gemmatum*, *Amanita muscaria*, *Calvatia saccata*, *Inocybe eutheloides*, *Lycoperdon pulcherrimum* and *Cortinarius sp* Twenty-eight of these fruit-bodies were imbedded in paraffin, sectioned and stained, and examined under the microscope for evidence of actual connection between fruit-body and root cells The results obtained in this examination will be described very briefly

Sections were made longitudinally through the stipes of the fruit-bodies and also transversely through the stipes In both types of sections the attached rootlets were sectioned longitudinally and transversely Many small roots were completely encircled by the mycelium of the stipe, but more typically the root tips were partly imbedded in the mycelium at one side or at the very base of the stipe When roots were encircled at some distance from their tips, it was not expected that any connection would be found between fruit-body and root cells, but when the fruit-bodies occurred directly at the root tips, such a connection was expected

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[1] An undescribed species which Dr C H Kauffman has had under observation for several years

Despite careful sectioning, staining and examination, the mycelium of a fruit-body could not be traced to the interior of a root Furthermore, the mycelium in the root and in the mantle around the root was of a decidedly different character from the mycelium of the fruit-bodies The mycelium composing the fruit-bodies was quite hyaline, sparsely septate, with but few clamp connections, and was about 2 or 3 microns in diameter The mycelium in the root and directly around the root in the fungal mantle was dark-colored, frequently septate, had numerous clamp connections, and was from 4 to 6 microns in diameter

It would appear that the fruit-body does not originate from the same mycelium that formed the mycorrhiza This may be explained either on the basis of chance association or on the basis of required association Hansteen-Cranner (3) found that the roots of higher plants excrete certain substances, especially phosphatids Barthel (1) reports that Wilson found that many species of bacteria are stimulated by root excretions, and Melin discovered that the growth of many species of fungi which do form mycorrhiza is vastly stimulated by contact with the roots of tree seedlings Masui has shown by micro-chemical methods that mycorrhizal roots have less of carbohydrates, amino-acids, phosphorus, potassium, ammonium, nitrates and tannin than uninfected roots and that young fruit-bodies of mycorrhizal fungi have large amounts of these substances There is some reason for believing that the fruit-bodies occur in attachment to root tips because they need certain substances obtainable only from living roots It may or may not be necessary to penetrate the root to secure these substances Finally, it frequently happens that more than one species of fungi are found on the same mycorrhizal rootlet. Fuchs (2) was one of the first to emphasize this fact The mycorrhiza might be formed by a species which does not fruit very readily, and the soil in these plantations contains an incredibly large amount of mycelium On the whole, there is a considerable quantity of circumstantial evidence to indicate that the fruit body and the mycorrhiza are produced by two different species of fungi

On the other hand, there is a possibility that the fruit-body and the mycorrhiza were produced by the same fungus Old mycelium usually is darker than young mycelium and it may be that the mycelium which is in the root and in the mantle around the root, being older than that of the fruit-body, has taken substances from the root which would be responsible for the dark color and large size of this mycelium To make certain that staining did not cause the observed difference in color, several kinds of stain were used, and a number of slides were left unstained Though obviously not so pronounced in the unstained slides, the differences between the mycelium from the two sources were quite apparent All told, over one hundred slides were examined with precisely the same results, namely, that the mycelium in the root was totally different from the mycelium of the fruit-body, and in no instance could the mycelium of the fruit-body be traced inside the root

SUMMARY

1 Microscopic sections were made of twenty-eight fungus fruit-bodies with attached mycorrhizal rootlets These were examined under the microscope to learn whether the apparent attachment of fruit-bodies indicated a real connection with the interior of the roots and, therefore, constituted proof that these fungi are mycorrhiza-formers

2 The mycelium of the fruit-body could not be traced to the interior of the mycorrhizal rootlets

3 The mycelium inside the mycorrhizal rootlet and in the fungal mantle immediately around the root was of an entirely different character from the mycelium composing the fruit-body It is not known whether these differences are due to the presence of different fungi, or whether the two kinds of mycelium actually are the same fungus and the differences due to the age of the mycelium and to the presence of substances extracted from the roots

4 Although circumstantial evidence is often very strong, the apparent attachment of fruit-bodies to tree roots cannot be taken

as proof that the fungus forming the fruit-body likewise formed the mycorrhiza Proof of this must be established through microscopic investigation

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LONGEVITY OF CONIDIA OF COMMON FUNGI UNDER LABORATORY CONDITIONS

ADELIA McCREA

THE problem of longevity in spores of fungi has been studied very little and chiefly in a desultory way.[1] It is known, however, that in some species these minute resistant cells, when dried, are able to survive very unfavorable conditions for a long time. Several years ago the writer reported (*Science*, 58: 1508. 1923) that conidia of *Aspergillus oryzae* and *Rhizopus nigricans* were still viable after having been sealed in a glass tube and kept in an office safe for twenty-two years. They had been collected as thoroughly dry spore dust, entirely free from the substratum. Tests made at that time showed that the *A. oryzae* strain still possessed normal diastatic activity, and Dr. Neil E. Stevens, in a personal communication, reported that the *R. nigricans* subculture retained typical capacity for causing "leak" of strawberries.

Eight years later, i.e. thirty years from the time the spores were first collected, the seal was again removed and transplants were made. Cultures of both organisms were obtained without difficulty. The tube was resealed at that time (1927) and will be opened again after a lapse of five years.

The present note concerns a group of common "laboratory weeds" of the mold fungi. Such cultures are isolated from various sources and gradually accumulate in considerable numbers. In the course of routine work, several species in test-tube cultures were recently checked for viability after having been stored from eight to ten years in opaque boxes under laboratory conditions. They were originally planted upon Sabouraud's medium prepared from ingredients of American manufacture. This choice of substratum has no special significance except that it has proved very useful in maintaining the characteristics of a culture with a minimum of labor. Cultures require transplanting only three or four times in a year.

Fifty-five cultures which were planted in 1919, 1920, 1921 or 1922, and hence had long been thoroughly dry, were used in this series for a test of viability persisting eight to ten years. Of these, twenty-five grew in normal manner. The remaining thirty are probably dead. Twelve species (marked with an asterisk) are included among the twenty-five cultures which survived the prolonged drying. Some species appear more than once in the following table, having been collected at various times and places, e.g. *A. niger*, of which there were seven strains.

The old cultures from which living transplants were obtained will be kept for future tests, so that eventually the period of viability may be extended for some or all of these species. The tubes have not been sealed, nor was any process such as soaking of spores resorted to. Each of the cultures herein listed is the result of a simple transfer of the old material to fresh food, due care being taken to prevent all chance of contamination.

TABULATION OF CULTURES

The species marked with an asterisk (*) are those which survived the prolonged drying. Others are duplicates isolated from various sources.

Alive after ten years

Culture number	Organism
12	*Aspergillus glaucus Link
16	*Penicillium chrysogenum Thom
33	*A. fumigatus Fres.
46	*A. niger Van Tieghem
76	A. glaucus Link
105	A. niger Van Tieghem
142	*A. wentii Wehmer

Alive after nine years

24	*A. versicolor Vuillemin
56	*Mucor racemosus Bull
59	A. niger Van Tieghem
85	A. fumigatus Fres.
149	A. niger Van Tieghem

live after eight years

Culture number	Organism
2	A niger Van Tieghem
13	*P expansum Link
17	*P commune Thom
25	P expansum Link
51	*A flavus Link
57	*Fusarium roseum Link
58	A glaucus Link
81	A niger Van Tieghem
99	*A oryzae (Ahlburg) Cohn
102	F roseum Link
103	F roseum Link
174	A niger Van Tieghem
189	A wentii Wehmer

PARKE, DAVIS AND COMPANY
DETROIT, MICHIGAN

SOME PLANTS THAT WERE PROBABLY BROUGHT TO NORTHERN OHIO FROM THE WEST BY INDIANS

EDWIN LINCOLN MOSELEY

ON THE peninsulas that border Sandusky Bay on the north and east and on the neighboring islands in Lake Erie there are thirty species and varieties of spermatophytes not found elsewhere in the Sandusky flora A few of these have been found nowhere else in Ohio, and a few others are known to grow in only one or two other localities in the state Some of them may have been borne there by water from the region of the Upper Lakes and seeds of a few kinds may have been blown there from many miles away

Cactus, *Opuntia rafinesquii*, has been growing on these two peninsulas, and also on the mainland four miles southwest of Sandusky, so long that no one seems to know when or how the plants got a foothold there The only other habitats known to me nearer than Muskegon County, Michigan, are Point Pelee, which is across Lake Erie from Sandusky, and a spot in Wood County, Ohio, eight miles east of Bowling Green, where this cactus has been growing on a low sand ridge at least since the childhood of old inhabitants After John Young Fish settled here, about 1832, this spot in Wood County was still a camp site for the Indians One of my pupils who lives near it has found there many Indian stone implements, far more than he has found elsewhere in Ohio Less than half a mile east of the cactus was found an Indian grave in which was a copper kettle, a hatchet with a pipe bowl hollowed from the top, and a skull in which was sticking a stone arrow point Close to where the cactus is growing the Indians long ago used to sit in the sand and shape arrow points, as I have been told by Harry Fish, whose grandfather owned the land at that time A man who still lives near has a large collection of stone implements found there

From the narrative of one James Smith, who, when a young man, was captured by Indians in western Pennsylvania about the time of Braddock's defeat and accompanied them in their migrations for several years, we learn that the Sandusky region was a favorite place for hunting, fishing and raising crops. On Kelley's island, which forms a part of the same county, is the most famous example of Indian picture writing known Here large numbers of their stone implements have been found Four miles from here, on the Marblehead Peninsula, there were many Indians living in 1809 and later They used to swim their ponies across the channel, which at times of very low water was only 300 feet wide, to Cedar Point At that time this must have been a common route of travel from west to east, just as the bridges across Sandusky Bay are now Cactus, whose fruit was appreciated by the Indians, may have been carried in their journeys and its seeds scattered where they camped, or they may have purposely planted the seeds in the isolated localities where it still grows in this part of North America

A plant whose light seeds may have been brought east by the Indians because of their merely getting into some of their paraphernalia is *Actinea herbacea* (Greene) Robinson = *Actinella acaulis glabra* Gray = *Picradenia* Hook = *Tetraneuris* Greene This has grown on the Marblehead Peninsula so long that no one knows when it started there, although it has spread noticeably even within the past forty years It is not known elsewhere east of Nebraska, except at Joliet, Illinois, where it is also spreading There it was first found on an Indian mound The natural route to the Great Lakes from the Mississippi was by way of the Illinois and Desplaines rivers to the Chicago River At the portage, near Joliet, naturally there would be a camp site and unpacking and packing of goods Here there has recently been found one of the most interesting successions of prehistoric remains yet discovered in this part of North America

The lotus, *Nelumbo lutea,* produces edible tubers and seeds which were important in the diet of the Indians By them it was much sought and highly prized They even invested it with mystic powers The plant has been growing in a number of isolated localities between Illinois and the Atlantic Ocean so long that dissemination by the Indians seems to be the only reasonable explanation Beal and Wheeler give only one locality for the interior of Michigan McCoun, when his *Catalogue of Canadian Plants* was published, had never seen the lotus in Canada, but had heard of it in three places, all within a few miles of Lake Erie The total quantity of Nelumbo growing in all localities farther east in the United States and Canada, together with that in the interior of Indiana and Michigan, is probably much less than that which grows in the Sandusky region and near Lake Erie between Sandusky and Monroe, Michigan In the marshes east of Sandusky the plant formerly grew in such profusion that some enterprising high school lads were able to realize a good income from the opening blossoms, which they gathered and sent to Cleveland

The ovate-leaved New Jersey tea or redroot, *Ceanothus ovatus*, is another plant which was probably distributed by Indians From its leaves they made tea and from the woody, gnarled roots, because of their toughness, they made balls for their shinny games It was called *tabe hi*, "ball plant," by the Omaha and Osage tribes It is rare in Michigan and Canada In Indiana it grows only on sand ridges south of Lake Michigan There is — or was — a good deal of it on the Marblehead Peninsula north of Sandusky

Symphoricarpos pauciflorus has been found nowhere in Indiana, nor in Canada east of Lake Superior, and in only two localities in Michigan — Harbor Springs, Keweenaw County, and Hubbardston, Ionia County In Ohio it is — or was — common on the Marblehead Peninsula and across the channel on Cedar Point In this connection the name "Indian currant" for *Symphoricarpos orbiculatus* suggests that the Indians may have used the berries from plants of this genus They used an infusion of Indian currant leaves for weak or inflamed eyes

From the roots of *Gentiana puberula*, the prairie gentian, the Indians made a decoction which they used as a tonic Possibly they brought the seeds to the few isolated localities where the plant has been found in Michigan, Indiana and Ohio

The six species mentioned in this paper as examples of plants which the Indians may have brought to the localities where they camped are cactus, lotus, snowberry, ovate-leaved New Jersey tea, prairie gentian and *Actinea herbacea* Although some have spread locally, yet, so far as we know, they have not been able to reach other localities in the course of the many years of occupation by the white man without being carried and planted by him [1]

Ohio State College
Bowling Green, Ohio

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[1] For information relating to the uses which the Indians made of these plants the writer is indebted to Melvin R Gilmore

FUNGI OF ROCK RIVER, MICHIGAN

ALFRED H POVAH

THE writer spent approximately three weeks, during the late summer of 1927, with an expedition from the University of Michigan Herbarium at Rock River, Alger County, Michigan, collecting and studying the fungi of that region Owing to illness, his work was not included with the results of the other members of the expedition, published by Kauffman (3) Since the collecting was done independently and since the work of the author resulted in supplementing Kauffman's list by over one hundred species, it is deemed advisable to record it An asterisk placed before the name of a species denotes that it was reported by Kauffman as well as by the writer An approximate index, therefore, of the frequency of any given species may be shown by its occurrence in both lists

The specimens are in the author's herbarium, with duplicates, when available, in the University of Michigan Herbarium The identifications were made by the writer, with the exception of the collections of Poria, which Dr D V Baxter has named, the grass hosts, which were determined by Dr B B Kanouse, and a few other specimens, for the identifications of which credit is given in the list

MYXOBACTERIACEAE

MYXOCOCCUS CORALLOIDES Thaxt — On deer dung

MYXOMYCETES

*ARCYRIA INCARNATA Pers — On old white cedar log

CRIBRARIA AURANTIACA Schroed — On very rotten log

DIDERMA ASTEROIDES List — On decaying twigs and leaves

DIDERMA CRUSTACEUM Pk — On rotten stick

Fuligo cinerea (Schw) Morg — On rotten birch log

Fuligo intermedia Macbr — On rotten log

Physarum vernum Somm — On rotten log

***Stemonitis axifera** (Bull) Macbr — On birch log

Stemonitis fenestrata Rex — On old coniferous log

Stemonitis fusca (Roth) Rost — On old spruce log

Stemonitis Smithii Macbr — On tips of *Sphagnum sp*

***Stemonitis Webberi** Rex — On birch log

***Tubifera ferruginosa** (Batsch) Morg — Common on rotten wood

PHYCOMYCETES

Absidia orchidis (Vuill) Hagem — On insect remains Cultured

Mucor circinelloides Van Tiegh — Isolated from Sphagnum

Pilobolus sp — On deer dung

***Endogone sphagnophila** Atkins — Common on tips of Sphagnum and occasional on decaying leaves

Empusa apiculata Thaxt — On *Culex sp* Common

Empusa culicis A Braun — On *Culex sp* This and the preceding Culex-inhabiting species were very abundant on the under side of logs and stumps in swamps drying up Both conidial and zygosporic stages

Entomophthora rhizospora Thaxt — Common on caddis flies

Physoderma Menyanthis de By — Parasitic on *Menyanthes trifoliata* L

ASCOMYCETES

DISCOMYCETES

Geoglossaceae

Cudoniella coniocyboides Rehm — Growing on mycorrhiza in white cedar swamp Mycorrhiza ectotrophic, fungous mantle 20–70 μ wide Cap "cream buff" to "ochraceous tawny" (R) 1–2 mm in diameter, margin slightly lobed, stalk 3–6 mm long, 0 3–0 5 mm in diameter

Geoglossum glabrum Pers — In sphagnum bog
Helvella elastica Bull — In swamp Det C H Kauffman
Helvella infula Schaeff — In swamp Det C H Kauffman
Microglossum fumosum (Pk) Dur — On much-decayed wood in cedar swamp
Mitrula cucullata (Batsch) Fr — On fallen leaves of conifers Durand (2) reports this for the northeastern United States, i e Maine, New Hampshire and New York
*Sphathularia velutipes Cke & Farl — On rotten birch log

Pezizaceae

*Lachnea leucotricha (A & S) Quél — On soil
*Lachnea scutellata (F'k'l) Gill — On rotten wood
Lachnea stercorea Pers — On deer dung
Lachnea theleboloides (A & S) Gill — On dung
*Lamprospora Crec'hqueraultii (Crouan) Boud — On white birch log
*Macropodia macropus (Pers) F'k'l — On rotten wood
Plicaria repanda (Wahlb) Rehm — On white birch log

Ascobolaceae

Ascobolus stercorarius (Bull) Schroet — On dung
Ascophanus Aurora (Crouan) Boud — On deer dung
Ascophanus cervinus, sp nov

Apothecia orange, 1–3 mm in diameter, gregarious, asci cylindrical 144–160 × 8–11 μ (spor pt 83–90 × 8–11 μ) 8-spored, spores hyaline, elliptical 12 5–16 × 6–8 μ, paraphyses branched, filiform but slightly enlarged at the apices Collected September 10, 1927, at Rock River, Michigan, on deer dung Type in Povah Herbarium and in University of Michigan Herbarium

This species is closely related to *Ascophanus Aurora* (Crouan) Boud, but differs in having larger apothecia, more slender asci and longer spores

Lasiobolus equinus (Muell) Karst — On deer dung
Lasiobolus longisetosus Povah — On deer dung
Thelebolus Zuckalii Heinn — On deer dung

HELOTIACEAE

Chlorosplenium aeruginosum (Oeder) de Not — On old log

Chlorosplenium versiforme (Pers) Karst — On rotten log

Coryne sarcoides (Jacq) Tul var **viridescens** Rehm — On white birch stump

****Dasyscypha Agassizii** (B & C) Sacc — On dead *Abies balsamea*

****Helotium citrinum** (Hedw) Fr — On wood of frondose species

****Lachnum virgineum** (Batsch) Karst — On old stick

Lachnum viridulum Massee & Morg — On rotten log Apothecia 0 3-0 6 mm diam , asci 41–54 × 8–11 μ, spores 12–14 × 2–3 μ The specimens are referred to this species although asci and spores do not quite fit Massee and Morgan's (7) measurements

****Ombrophila enterochroma** (Pk) Sacc — On decaying leaves in swamp

Ombrophila hirtella Rehm — On decaying leaves in swamp

Ombrophila janthina Karst — On decaying leaves and branches of conifers in swamp When fresh the color is "light grayish vinaceous" (R) The asci measure 60–85 × 6–8 μ, the spores are 5–8 × 2 5–3 μ

Phialea virgultorum (Vahl) Sacc — On fallen twigs in swamp

PHACIDIACEAE

Clithris degenerans (Fr) Rehm — On dead stems of *Chamaedaphne calyculata* Det C L Shear This is a new host, Saccardo (8) gives *Vaccinium uliginosi* and *V corymbosi* and Seymour (10) gives *Andromeda sp* in addition to these two species of *Vaccinium*

Rhytisma acerinum (Pers) Fr — On *Acer sp*

Rhytisma andromedae (Pers) Fr — On *Andromeda glaucophylla* Pk

****Rhytisma ilicis canadensis** Schw — On *Nemopanthes mucronata*

Rhytisma salicinum (Pers) Fr — On *Salix sp*

HYPODERMATACEAE

LOPHODERMIUM OXYCOCCI (Fr.) Rehm. — On leaves of *Vaccinium Oxycocci*.

LOPHODERMIUM SPHAERIOIDES (A. & S.) Duby. — On decaying leaf of *Ledum groenlandicum*.

PYRENOMYCETES

GYMNOASCACEAE

GYMNOASCUS UNCINATUS Eidam. — On deer dung. See Figure 12.

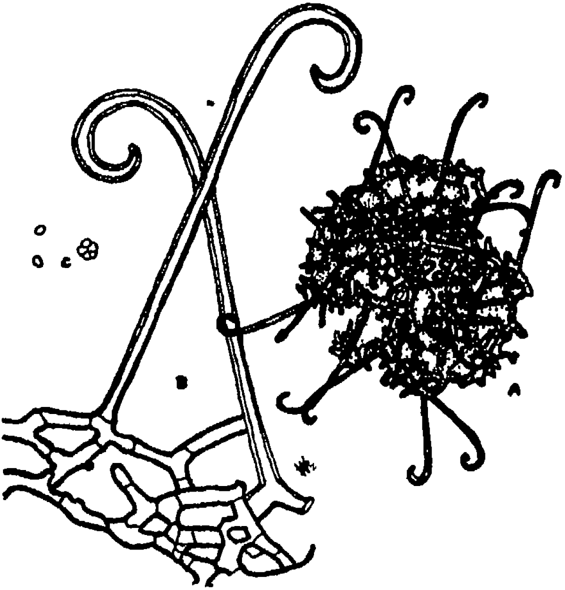

FIG. 12. *Gymnoascus uncinatus* Eidam. — *A*, habit, low power; *B*, portion of net with two uncinate appendages, high power; *C*, ascus and spores, high power.

ERYSIPHACEAE

UNCINULA SALICIS (D C) Wint — On *Salix sp*

PERISPORIACEAE

CAPNODIUM PINI B & C — On living *Pinus Strobus* Only imperfect stage

HYPOCREACEAE

CLAVICEPS MICROCEPHALA (Fr) Tul — On *Phleum pratense*

*CLAVICEPS PURPUREA (Fr) Tul. — On *Danthonia spicata* (L) Beauv , *Agrostis alba* L and on *Phalaris canariensis* L Kauffman (3) reported this fungus on different hosts

CORDYCEPS FORMICIVORA Schroet — On *Formex ligniperda* A single ant was collected which had two "seal brown" (R) stromata, 1 5 mm in diameter attached by slender stalks, 0 75 mm long, one to each side of the top of the ant's head The asci measure 170–191 × 6–7 μ, the spores are hyaline, filiform, curved and measure 80–102 × 2 5–3 μ Apparently no record of an American collection is in the literature A letter to Dr C L Shear brought out the fact that no American collection is in Washington Professor Thaxter wrote in reply to an inquiry "I was interested in your record of *C formicivora* which seems a characteristic species and which I have found on several occasions in York, Maine, on the same species of ant which it attacks in Europe It occasionally produces a pure white Isaria-condition "

CORDYCEPS MILITARIS (L) Lk — On remains of insect in swamp

*NECTRIA BALSAMEA Cke & Pk — On *Abies balsamea*

NECTRIA EPISPHAERIA (Tode) Fr — Parasitic on *Hypoxylon fuscum* (Pers) Fr

CHAETOMIACEAE

CHAETOMIUM COCHLIOIDES Palliser — On paper (label) and wax-paper wrapping of collection of deer dung

Chaetomium Kauffmanianum, sp nov (Fig 13)

Perithecia (Fig 13*A*) brownish-black, ovate, 283–372 × 182–294 μ, attached to the substratum by a tangled mass of

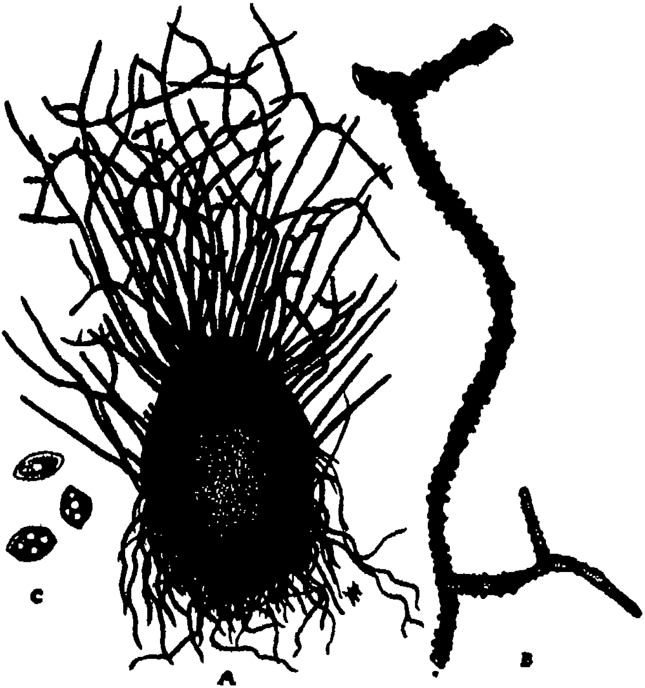

FIG 13 *Chaetomium Kauffmanianum* Povah — *A*, habit sketch of perithecium, *B*, portion of terminal hair much enlarged, *C*, spores

dark brown, flexuous, simple or sparsely branched, and pauci-septate hairs, 2 5–3 μ in diameter at the base Lateral hairs not numerous, long, unbranched, near the base roughened with warts or tubercles, brownish-black, about 4 μ in diameter, gradually tapering and becoming paler toward the pale brown, septate tips Terminal hairs roughened with warts or tubercles (Fig 13*B*), simple or 1–3 times dichotomously branched, with the branches widely diverging and irregularly once or twice forked, at the base brownish-black and approximately 4 μ in diameter, tapering and becoming paler toward the tips Asci evanescent, 8-spored, distichous Spores dark brown, lemon-shaped, apiculate at both ends (Fig 13 *C*), 9–10 × 6–7 μ, when viewed laterally compressed, 5 μ broad, with several (3–5) guttulae

The fungus developed on the label (paper) and wax-paper wrapping of a collection of deer dung made on September 10, 1927, at Rock River, Michigan Type in Povah Herbarium and University of Michigan Herbarium

This species is related to *C elatum* Kunze and Schmidt, from which it differs in the smaller perithecia, more delicate terminal hairs and smaller spores It is named in honor of Professor C H Kauffman

SPHAERIACEAE

BOMBARDIA FASCICULATA Fr — On rabbit dung This fungus is recorded as occurring on wood rather than dung However, the curious spores, hyaline and worm-shaped when young but becoming at maturity dark brown with a very long, hyaline appendage, are characteristic

CERATOSTOMATACEAE

CERATOSPHAERIA ROSTRATA (Kickx) Sacc — On decorticated wood

AMPHISPHAERIACEAE

AMPHISPHAERIA THUJINA (Pk) Sacc — On decaying white cedar leaves

LOPHIOSTOMATACEAE

LOPHIOSTOMA THUJAE E & E — On dead white cedar

PLEOSPORACEAE

LEPTOSPHAERIA CREPINI (West) de Not — On strobili of *Lycopodium annotinum* L

LEPTOSPHAERIA LYCOPODICOLA Pk — On strobili of *Lycopodium annotinum* and *L complanatum* var *flabelliforme* Apparently these are new hosts for this fungus, which is reported on *L clavatum*

VALSACEAE

*ANTHOSTOMA MICROSPORUM Karst — On *Alnus incana* (L) Moench

VALSA LEUCOSTOMA (Pers) Fr — On *Populus tremuloides* Michx

XYLARIACEAE

DALDINIA CONCENTRICA (Bolt) Ces & de Not — On *Alnus sp* The spores in our collection, which measure 11–13 × 4 8–5 7 μ, are smaller than those given for this species

HYPOXYLON ALBOCINCTUM E & E — On birch and red maple The stroma is at first "clay color" (R), becoming "Saccardo's umber" (R) and at length "clove brown" (R)

*HYPOXYLON FUSCUM (Pers) Fr — On alder and red maple

*HYPOXYLON MULTIFORME Fr — On white and yellow birch

HYPOXYLON PRUINATUM (Klotsche) Cke — On *Populus tremuloides*

*HYPOXYLON RUBIGINOSUM (Pers) Fr — On decorticated wood

FUNGI IMPERFECTI

CEPHALOTHECIUM ROSEUM (Fr) Cda — On old leaves and on dung

*CYTOSPORA CHRYSOSPERMA (Pers) Fr — On maple

MACROPHOMA SPARTIICOLA Berl & Vogl — On *Agrostis alba* L

MACROSPORIUM PINGUEDINIS Berk — On *Calamagrostis canadensis* (Michx) Beauv

Monilia ochracea, sp nov

"Warm buff" (R) to "yellow ochre" (R) effuse, extending 8 × 2 5 cm., pulverulent, hyphae much-branched and tangled (Fig 14*A*), septate, yellow, 6–7 μ in diameter, fertile hyphae up to 700 μ long, erect (Fig 14*B*), bearing simple or branched chains of elliptical or citriform, pale yellow spores (Fig 14*B*, *C*) measuring 11–19 × 6–8 μ

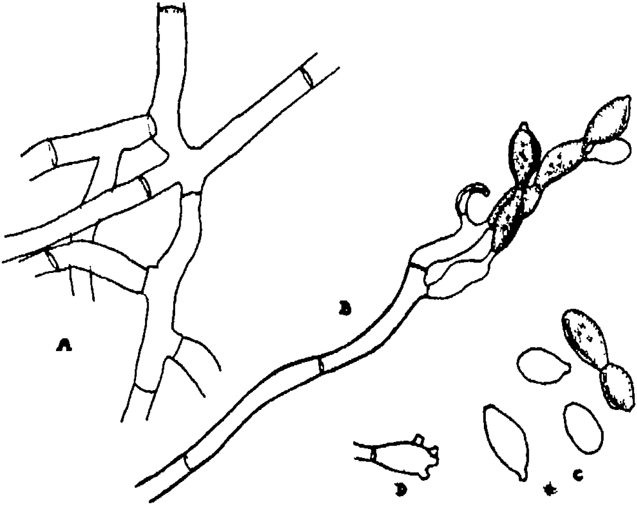

FIG 14 *Monilia ochracea* Povah — *A*, fragment of mycelium, showing branching and septation, *B* terminal end of conidiophore, with catenulate conidia, *C*, spores, *D*, terminal cell of conidiophore, with sterigmata All high power

Collected on September 5, 1927, at Rock River, Michigan, on an old coniferous log Type in Povah Herbarium and University of Michigan Herbarium

*SPHAERONEMA ACERINUM Pk — On maple

*SPHAERONEMA PRUINOSUM B & C — On *Amelanchier sp*

Sphaeropsis abietis, sp nov

Pycnidia superficial, gregarious, globose-subglobose, 75–90 (55–110) μ in diameter Spores grayish, elliptical, 13–16 × 5–6 μ Type collected August 22, 1927, at Rock River, Michigan, on leaves of a dead branch on a living tree of *Abies balsamea* Type in Povah Herbarium and University of Michigan Herbarium

THAXTERIOLA SUBHYALINA Speg — On nitidulid (?) beetle Det R Thaxter In a letter Professor Thaxter says "I do not feel sure that there is more than one species, perhaps two It [*T subhyalina*] is more or less ubiquitous and omnivorous and may be somewhat lighter or somewhat darker with variations in the straightness or curvature of the neck"

VERTICILLIUM BOTRYOIDES Sacc — On *Physarum sp*

VERTICILLIUM GLAUCUM Bon — On wood-cutting ant and on old log

BASIDIOMYCETES

UREDINALES

*CALYPTOSPORA COLUMNARIS Kuehn III — Forming witches'-brooms on *Vaccinium sp*

DICAEOMA CLEMATIDIS (DC) Arth I — On *Clematis virginiana* L, II and III — On *Elymus virginicus* L

DICAEOMA RHAMNI (Wettst) O Kuntze III — On *Calamagrostis canadensis* and *Cinna latifolia* (Trev) Griesb

MELAMPSORA HUMBOLDTIANA Speg — On *Salix sp*

*MELAMPSOROPSIS CASSANDRAE (Tranz) Arth & Jacks I — On *Picea Mariana* (Mill) BSP, II and III — On *Chamaedaphne calyculata*

MICROPUCCINIA MESOMEGALA (B & C) Arth & Jacks — On *Clintonia borealis* (Ait) Raf

PILEOLARIA TOXICODENDRI (B & Rav) Arth — On *Rhus Toxicodendron* L

UREDINOPSIS OSMUNDAE Magn — On *Osmunda regalis* L

TREMELLALES

CALOCERA CORNEA Fr — On old log

CALOCERA PALMATA (Schum) Fr — On old poplar wood

CALOCERA VISCOSA (Pers) Fr — On rotten log

EXIDIA GLANDULOSA Fr — On *Populus tremuloides* and on dead alder

GUEPINIA SPATHULARIA (Schw) Fr — On old spruce log

AGARICACEAE

*Armillaria mellea (Vahl) Sacc — On hemlock
Cantharellus cibarius Fr — In coniferous woods
Clitocybe laccata Fr var amethystina Bolt
*Cortinarius armillatus Fr
Hygrophorus miniatus Fr
Hypholoma perplexum Pk — On *Betula lutea*
Lentinus lepideus Fr — On coniferous wood
*Marasmius androsaceous (L) Fr
Marasmius rotula (Scop) Fr — On birch log
Mycena amabilissima Pk
Omphalia campanella Fr — On white cedar log
*Pholiota squarrosoides Pk — In wound on living *Betula lutea*
*Pleurotus porrigens Fr — On rotten log Det Kauffman
*Pleurotus serotinus Fr — On yellow birch
Pluteus cervinus Schaeff — On birch
*Pluteus leoninus Pk — On rotten log
Russula nigrodisca Pk — On ground under conifers at Little Lake, Michigan Det C H Kauffman
Schizophyllum commune Fr — On *Prunus sp*

BOLETACEAE

*Boletinus paluster Pk — Common on wood in sphagnum bog

CLAVARIACEAE

Clavaria cristata (Holmsk) Pers — In sphagnum under white cedars
Clavaria muscoides L — In cedar swamp

HYDNACEAE

*Asterodon ferruginosum Pat — On spruce and birch logs
Hydnum albonigrum Pk — Det Kauffman On ground under conifers
Hydnum caput-ursi Fr — On old log
Hydnum ochraceum Pers — On *Alnus sp* and on *Betula alba*
Hydnum repandum Linn — In coniferous forest

IRPEX SINUOSUS Fr — On *Alnus incana*

ODONTIA AMBIGUA Karst — On rotten coniferous log The spores are hyaline, globose-subglobose, 3–5 μ in diameter, each containing one large oil drop

*PHLEBIA STRIGOSO-ZONATA (Schw) Lloyd — On poplar

RADULUM BENNETTII B & C — Under bark on spruce log

THELEPHORACEAE

ALEURODISCUS AMORPHUS (Pers) Rabenh — On dead balsam fir

*EXOBASIDIUM VACCINI (F'k'l) Woron — On *Vaccinium sp*

HYMENOCHAETE AGGLUTINANS Ellis — On *Betula lutea* and *Acer rubrum*

*HYMENOCHAETE TABACINA (Sowerb) Lév — On *Thuja occidentalis*

HYPOCHNUS CERVINUS Burt — On burnt pine log Burt (1) records a single collection of this species on maple from Washington Notwithstanding the different host and locality, the author's collection has been referred to this species because of its thin, inseparable, fructification of "fawn color" (R), with whitish margin and the hyaline, nodose-septate hyphae

HYPOCHNUS FUMOSUS Fr — On old log of frondose species

HYPOCHNUS SUBFERRUGINEUS Burt — On *Thuja occidentalis*

HYPOCHNUS UMBRINUS (Fr) Burt — On decayed wood

PENIOPHORA CANDIDA (Pers) Lyman — On pine log (The absence of spores prevents an unquestionable determination)

PENIOPHORA CINEREA (Pers) Cke — On *Betula sp*

PENIOPHORA FILAMENTOSA (B & C) Burt — On yellow birch

PENIOPHORA INCARNATA (Pers) Karst — On *Populus tremuloides*

*STEREUM FASCIATUM Schw — On birch log

STEREUM MURRAYI (B & C) Burt — On yellow birch logs

*STEREUM RADIATUM Pk — On pine log

*STEREUM RUFUM Fr — On *Populus tremuloides*

*STEREUM SULCATUM Burt — On pine log

POLYPORACEAE

*DAEDALEA CONFRAGOSA (Bolt) Fr — On *Betula alba* var *papyrifera*

*Daedalea unicolor (Bull) Fr — On stick of frondose species

Fomes applanatus (Pers) Wall — On white birch, yellow birch and hemlock

Fomes connatus Fr — On living *Acer rubrum* L

*Fomes fomentarius (L) Gill — Common on white birch, yellow birch and poplar

*Fomes igniarius (L) Gill — On white birch

Fomes laricis (Jacq) Murr — On hemlock and spruce

*Fomes nigricans Fr — On yellow birch and on living beech

*Fomes pinicola Fr — On dead red maple and on spruce

*Fomes scutellatus (Schw) Cke — On *Alnus incana*

Lenzites betulina (L) Fr — On white birch

Lenzites sepiaria Fr — On spruce and pine logs

Lenzites vialis Pk — On old log

Merulius ceracellus (B & C) Overh — On old logs

Merulius fugax Fr — On birch and white cedar logs When fresh the color varies from "orange chrome" or "flame scarlet" to "zinc orange" (R)

Merulius niveus Fr — On alder

*Merulius tremulosus Schrad — On white birch

Polyporus adustus (Willd) Fr — On *Populus grandidentata*

*Polyporus albellus Pk — On white birch and alder

Polyporus alboluteus E & E — On coniferous log

*Polyporus alutaceus Fr — Lloyd (4) says Bresadola considers *P guttulatus* Pk as the same plant

Polyporus benzoinus (Wahlenb) Fr — On yellow and on white birch

*Polyporus betulinus (Bull) Fr — On white birch

*Polyporus brumalis (Pers) Fr — Common on white birch

*Polyporus elegans (Bull) Fr — On white birch and on alder

Polyporus fibrillosus Karst — On spruce stump

Polyporus focicula B & C — On sandy soil

Polyporus fumosus (Pers) Fr — On rotten log of frondose species

*Polyporus glomeratus Pk — Inside bark of white birch stub and on birch and maple logs

*Polyporus lucidus (Leys) Fr — On old pine stub and on hemlock

Polyporus mollis (Pers) Fr — On old coniferous log This specimen suggests *P ursinus* Lloyd, but the spores (3–4 × 0 7–1 μ) are too small Our specimens are but little discolored, although two are reddish-brown on the margin of the pileus The little discoloration is probably due to the fact that the specimens were dry when collected

Polyporus pargamenus Fr — On poplar and white birch

Polyporus perennis (L) Fr — Growing on sandy soil

*Polyporus picipes Fr — On maple

Polyporus pubescens (Schum) Fr — On dead yellow birch

*Polyporus resinosus Fr — On spruce log

Polyporus Rheades (Pers) Fr — On living *Populus grandidentata*

Polyporus Schweinitzii Fr — On exposed root of spruce

Polyporus sulphureus (Bull) Fr — On old log

*Polystictus abietinus Fr — On *Abies balsamea*

Polystictus hirsutus Fr — On red maple

*Polystictus velutinus Fr — On white birch

Polystictus versicolor (L) Fr — On birch log

Poria carbonaria B & C — On charred wood of pine and white cedar

*Poria ferrea (Pers) Romell – On poplar twigs A collection from maple shows numerous cystidia, otherwise it is characteristic

*Poria ferruginosa (Schrad) Fr — On red maple and white cedar

Poria laevigata Fr — On birch

Poria ornata Pk — On log of frondose species

Poria papyracea (Schw) Cke — On white cedar

*Poria prunicola Murr — On dead *Prunus sp*

*Poria rufa Fr — Common on spruce logs

*Poria subacida Pk — This very common species was collected on birch, spruce and burnt pine logs

*Poria vulgaris var calceus Fr (sensu Romell) – On charred logs of pine and white cedar

*Porothelium fimbriatum (Pers) Fr — On rotten log

*Solenia anomala (Pers) Fr — On log of frondose species

*Trametes carnea (Nees) Cke — On pine and on charred log

Trametes Morgani — On dead red maple Saccardo (9) gives this as a synonym of *T micans* (Ehrn), but Lloyd (5) says it is distinct

*Trametes pini Fr — On spruce and other conifers

Trametes quercina Lloyd — On log of frondose species Lloyd (6) named this species from material which the author collected in southern Michigan Since this later collection is more fully developed than the type collection, and since the original description is incomplete, it seems advisable to give an emended description from the Rock River material.

Pileus corky, sessile or effuso-reflexed, imbricate, 6–11 × 1 8–3 5 × 1 5–4 cm , white when fresh becoming "cinnamon buff" with zones of "clay color," "tawny olive" or "Saccardo's umber" (R), villous or hirsute, margin thin, "light buff" (R) sterile below, context white or pallid, 2–12 mm thick, tubes 2–9 mm long, the mouths white turning brownish when bruised, angular or round, 2–3 per mm , spores hyaline, straight or slightly curved, 5–7 5 × 2–2 5 μ, hyphae 3 μ in diameter The fungus is fragrant when fresh, but when dry has only a slight odor suggesting that of cucumbers

Trametes tenuis Karst — On birch Det D V Baxter

Trametes variiformis Pk — On burnt pine log

GASTEROMYCETES

Bovista pila B & C — On ground at Little Lake, Michigan

Lycoperdon pyriforme Schaeff — On rotten log

Nidularia pisiformis Roth — On sticks and decaying leaves

Harvard University

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VECTOR METHODS AS A BASIS FOR MATHEMATICAL FORMULATION OF THE DATA OF OENOTHERA GENETICS *

JOHN FITZ RANDOLPH

I

EXTENSIVE work on the inheritance of Oenothera and allied forms has shown that in many cases the offspring take the characteristics of the pistillate parent regardless of the pollen parent, or vice versa Bartlett's[1] and his associates' work on *Oenothera pratincola* and *Oe Reynoldsii* and their mutations has shown matroclinic inheritance in a most exhaustive system of crosses and backcrosses, whereas the work of DeVries[2] on *Oenothera biennis* and *Oe syrticola* provides a case of patroclinic inheritance These are merely examples from a considerable literature, chosen because of their familiarity There are, however, some who still seem to feel that the part of Oenothera work which does not follow the well-established Mendelian laws must be faulty in method or interpretation George H Shull,[3] himself engaged in Oenothera investigation, has led in this attitude

If, then, the "oenotherists," if they may thus be termed, who have not been able to bring their results into conformity with the conventional explanation of inheritance, could find some mathematical law that Oenothera strictly follows, one considers whether their work would not be given more attention To aid the formulation of such a law this paper is written, using some of the principles of vector analysis for a mathematical basis The cross-product and some of its immediate consequences are particularly applicable It brings out strict analogy between the Oenothera phenomena and other natural phenomena, and indicates that the regularities of inheritance observed in the non-Mendelising Oenothera crosses are capable of mathematical formulation, even though not by simple algebra, as in Mendelism

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* Paper from the Department of Botany of the University of Michigan, No 318

[1] Bartlett, H H, "Mass Mutation in *Oenothera pratincola*," *Bot Gaz*, 60 425–456. 1915

[2] DeVries, Hugo, "Über doppeltreziproke Bastarde von *Oenothera biennis* L und *O muricata* L," *Biol Centralbl*, 31 97–104 1911

[3] Shull, George H, "Linkage with Lethal Factors the Solution of the Oenothera Problem," *Eugenics, Genetics and the Family*, 1 86–99 1923

VECTORS

II

In order to understand the laws, consider first Gibbs and Wilson's[4] explanation of vectors

> In mathematics and especially physics two very different kinds of quantities present themselves Consider for example mass, time, density, temperature, force, displacement of a point, velocity and acceleration. Of these quantities some can be represented adequately by a single number — temperature by degrees on a thermometric scale, time, by years, days, or seconds, mass and density by numerical values which are wholly determined when the unit of the scale is fixed On the other hand the remaining quantities are not capable of such representation Force to be sure is said to be feet per second, but in addition to this each of them must be considered as having direction as well as magnitude. A force points North, South, East, West, up, down or in some intermediate direction The same is true of displacement, velocity, and acceleration No scale of numbers can represent them adequately It can represent only their magnitude, not their direction
>
> Definition A *vector* is a quantity which is considered as possessing direction as well as magnitude
>
> Definition A *scalar* is a quantity which is considered as possessing magnitude but no direction.

A vector is usually represented by an arrow pointing in the direction in which the displacement is taking place and having a length equal to the magnitude The place where the vector starts is called the origin and where it stops is called the terminus A vector will be represented by **a** and its scalar value, or magnitude, by *a* Thus in Figure 15 the direction of vector **a** is plainly seen to be from P to P' and its magnitude is a Also, $2\mathbf{a}$ has the same direction as $\mathbf{a}$, but the magnitude is $2a$ The other vector, $-\mathbf{a}$, represents a displacement in the opposite direction, but has the same magnitude

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[4] Gibbs, J Willard, and Wilson, Edwin Bidwell, *Vector Analysis* Charles Scribner's Sons. New York, 1913

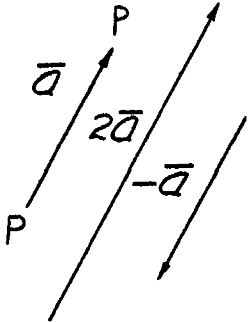

FIG 15

To move a vector from one point to another does not alter its value

If two vectors, say $\mathbf{a}$ and $2\mathbf{a}$, are added, a new vector in the same direction as $\mathbf{a}$, but three times as long, is formed This is shown in Figure 16 That is, if a force $\mathbf{a}$ is exerted on a load and then another force $2\mathbf{a}$, twice as great as the first and in the same direction, is added, the total amount of force exerted would be the same as if a single force three times as great as the first were applied in the same direction

If two parallel vectors are subtracted, say $2\mathbf{a} - \mathbf{a}$, the result is a vector of length (magnitude) a Also $\mathbf{a} - 2\mathbf{a} = -\mathbf{a}$.

If the vectors are not parallel, they can be represented as $\mathbf{a}$ and $\mathbf{b}$ The resultant of $\mathbf{a} + \mathbf{b}$ is defined as the long diagonal of a parallelogram of which $\mathbf{a}$ and $\mathbf{b}$ are sides (Fig 17) The reason for this can be seen by considering a load being pulled by two non-parallel forces, $\mathbf{a}$ and $\mathbf{b}$ If it is desired to do away with these two forces and apply a single force that will accomplish the same result, this can be done by using the diagonal of the parallelogram (Fig 17) as both direction and magnitude This is geometric addition in contrast to the usual algebraic addition If a steps are taken along $\mathbf{a}$ and then b steps along a line parallel to

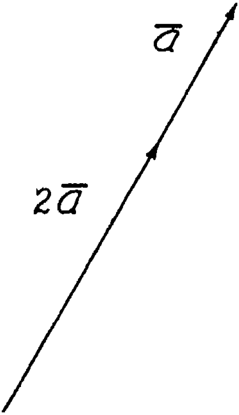

FIG 16

b, the point reached would be the same as taking $a^2 + b^2 - 2ab \sin \theta$ steps along the diagonal of the parallelogram determined by **a** and **b**

The vector **a** − **b** is the short diagonal of the parallelogram with direction and sense as indicated

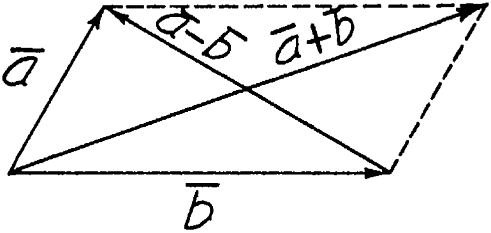

Fig 17

III

It has been assumed — the reason will be brought out later — that there is the same type of difference between the material on which "Mendelists" work and Oenothera, as far as inheritance is concerned, as there is between scalar and vector quantities That is, most plant and animal material follows scalar laws, but Oenothera possesses direction as well as magnitude in its breeding As will be shown later, the cytological work of Cleland, followed by that of Kulkarni, is demonstrating a mechanism of inheritance which shows why Oenothera inheritance is often directed, i e matroclinic or patroclinic

In scalar multiplication

$$2a \times 4b = 8ab,$$

or

$$(x + y)(x + y) = x^2 + 2xy + y^2,$$

and the geneticists say, correctly, that, if T = tallness (referring to Mendel's experiment of peas) and t = shortness and two F_1 individuals heterozygous for tallness are crossed, the result would be

$$(T + t)(T + t) = TT + 2Tt + tt,$$

where three F_2 individuals are tall and one is short On the other hand the oenotherists cannot say, Let $P =$ *Oe pratincola* and $p =$ *Oe numismatica*,[5] and the F_1 heterozygote be self-pollinated, and the result will be

$$(P + p)\,(P + p) = PP + 2Pp + pp,$$

with the F_2 generation consisting of three *Oe pratincola* and one *Oe numismatica*, for such a phenomenon is not observed

In the crosses above referred to the forms are two related species collected by Professor Bartlett in 1912 at Lexington, Kentucky, which have been studied in considerable detail by him and Dr Frieda Cobb Blanchard[6] because of the generally matroclinic inheritance of their mutations

What actually occurs is that *Oe pratincola* × *Oe numismatica* (following the convention of putting the female parent first) forms an F_1 of slightly modified *Oe pratincola*, which in turn, if allowed to self-pollinate, breeds true through any number of succeeding generations almost identical to a parallel culture that had *Oe pratincola* for both F_1 parents Still more interesting is it that the reciprocal cross *Oe numismatica* × *Oe pratincola* breeds pure *Oe numismatica* as consistently as the first bred *Oe pratincola* That is,

Oe pratincola × *Oe numismatica* → *Oe prat* → *Oe prat* →
Oe numis × *Oe prat* → *Oe numis* → *Oe numis* –

It is this phenomenon which has an analogy with the vector cross product which will now be given

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[5] The results of *Oe pratincola* and *Oe numismatica* crosses have never been published but were given to the author by Professor Bartlett They can be paralleled by the crosses of f *typica* and mut *semialta* of *Oe Reynoldsii* given later in this paper

[6] Cobb, Frieda, and Bartlett, H H, "On Mendelian Inheritance in Crosses between Mass-Mutating and Non Mass-Mutating Strains of *Oenothera pratincola*," *Journ Wash Acad Sci*, 9 462–482 Oct 4, 1919

IV

Definition

$$\mathbf{a} \times \mathbf{b} = \mathbf{c}\, ab \sin \theta,\text{[7]}$$

where $\mathbf{c}$ is a vector normal to the plane determined by $\mathbf{a}$ and $\mathbf{b}$ directed as a right-hand screw if turned from $\mathbf{a}$ to $\mathbf{b}$ through an angle θ less than 180° and having a magnitude equal to the area of the parallelogram determined by $\mathbf{a}$ and $\mathbf{b}$ This is shown diagrammatically in Figure 18, in which a solid must be visualised with the plane $\mathbf{a}$, $\mathbf{b}$ perpendicular to the plane of the paper, with $\mathbf{c}$ in the plane of the paper

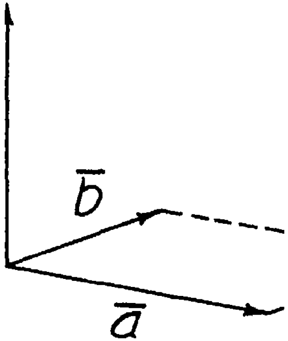

FIG 18

Notice that in $\mathbf{b} \times \mathbf{a}$ the screw direction will be opposite to that of $\mathbf{a} \times \mathbf{b}$, i e

$$\mathbf{b} \times \mathbf{a} = -\mathbf{c}\, ab \sin \theta$$

This would lead to Figure 19, in which the product vector has the same direction as that of Figure 18, but with the sense reversed

Out of this grows the general law

$$\mathbf{a} \times \mathbf{b} = -\mathbf{b} \times \mathbf{a},$$

a relation which has no counterpart in scalar mathematics

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[7] In vector analysis two products are used: the cross product $\mathbf{a} \times \mathbf{b}$ (here given) and the dot product $\mathbf{a} \cdot \mathbf{b}$ The dot, or scalar, product has no application here, and hence is not given

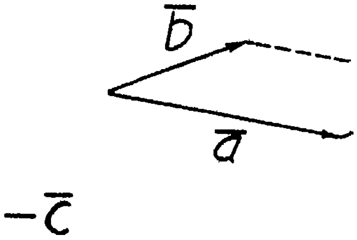

FIG. 19

VECTOR LAWS AS RELATED TO OENOTHERA [*]

V

Now by assuming that Oenothera possesses direction as well as magnitude in its inheritance an analogy with the vector cross product presents itself, that is, if **p** (= *Oe pratincola*) and **n** (= *Oe numismatica*) behave as vectors, the vector cross product finds a ready application. By "possessing direction," in this case, is meant that a zygote is not to be formed by a combination of any two gametes, but only by two which are complementary to each other, in that they may bring together particular combinations of chromosomes that are identical with parental combinations. It also means that at the reduction division there is no random disjunction of the two elements of chromosome pairs to either pole, but a necessity for chromosomes to disjoin in definite association.

It can then be said that

$$\mathbf{p} \times \mathbf{n} = \mathbf{c}\, pn \sin\theta,$$

which is experimentally known to be *Oe pratincola*. Also,

$$\mathbf{n} \times \mathbf{p} = -\mathbf{c}\, np \sin\theta,$$

---

[*] For simplicity, matroclinic inheritance alone will be considered.

which is *Oe numismatica* Further, since p and n behave as vectors, it will be true that

$$\mathbf{p} \times \mathbf{n} = -\mathbf{n} \times \mathbf{p},$$

which can be interpreted as reciprocal crosses, give reciprocal offspring Such a relation is essential to the mathematical formulation of Oenothera genetics, but since it could not be found in any field of scalar mathematics investigators were left with a feeling of uncertainty as to how their results could be formulated It has often been stated by those who were commenting upon the Oenothera results that they showed "some kind of regularity" If so, it should be possible to formulate them mathematically, and this paper is an attempt to indicate how it may be done

VI

Still more conclusive evidence is obtained by considering the further analogy between the alpha-beta hypothesis of Professor Bartlett and the vector cross product He assumed that in each somatic cell of Oenothera there are two chromosome complexes, which he called the α-gamete and the β-gamete Each complex consists of chromosomes organized in such a way that at the reduction division the α-chromosomes are drawn together at one pole while the β-group is formed at the other pole Moreover, in case there is elimination of either type of gametic complex at the reduction division, the female side has a distinct tendency to retain the α-group and discard the β-group This may happen as some obscure difference between the megaspore reduction and the microspore reduction, since in the former case there is a regular elimination of three out of four reduced cells At fertilization the β-sperm is either more strongly attracted to the egg than is an α-sperm[9] or else $\alpha\alpha$-combinations prove to be generally lethal Then, the gametes produced by a plant are like the ones which went into its own make-up, i e the gamete complex which came from the egg goes back into an egg while the gamete complex from the sperm goes back into the functioning sperms Direction must be taken into consideration in the formulation of such phenomena

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[9] Incidentally this follows the behavior expected if α- and β-chromosomes possess opposite electrical charges from the prophase until shortly after fertilization

The α-gamete is, then, the one that carries most of the differentiation genes that determine the specific distinguishing characteristics which the plant will take on and is, therefore, different for each species of a closely related group On the other hand the β-gamete is almost a blank as far as specific character determiners are concerned and hence is alike for many related species True, there are four known characters in the group of *Oe pratincola*, bud color, color of the axis of the inflorescence near the apex, viscid pubescence of the buds and revoluteness of the leaves, which are determined by the β-gamete, but these are so few and insignificant in comparison with those of the α-gamete that they need not be considered in this general discussion

Through the cytological examinations of *Oe pratincola* by Kulkarni,[10] it was found that the fourteen chromosomes emerge from the second contraction of the prophase connected end to end by delicate threads rather than in pairs, as in Mendelizing material During the metaphase this chain, which is generally closed, persists while the spindle fibers attach themselves in such a way as to draw alternate chromosomes to the same pole In the anaphase seven chromosomes are drawn toward each pole, the connections being broken between the members of the two separate groups as they near the poles, thus establishing two reduced nuclei, each with a definite combination of chromosomes Such a formation as this is essential to parallel Bartlett's alpha-beta hypothesis, just as the usual chromosome behavior parallels that of unit character inheritance in material following Mendelian laws The correlation of these findings with the genetical are still not worked out in detail, but enough has been done to warrant investigators in looking optimistically to future developments Cleland[11] is the leader in this field of work in America, and Renner[12] in Europe

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[10] Kulkarni, Chandrakant G , "Meiosis in Pollen Mother Cells of Strains of *Oenothera pratincola* Bartlett,' *Bot Gaz*, 88 218-259 March, 1929

[11] Cleland, Ralph E., ' Chromosome Arrangement during Meiosis in Certain Oenotheras," *Am Nat*, 57 562-566 1923

[12] Renner, O , "Untersuchungen über die faktorielle Konstitution einiger komplex-heterozygotischer Önotheren," *Bibliotheca genetica*, 9 168 pages, 58 text figures.

VII

The correlation of the alpha-beta hypothesis and the vector behavior of Oenothera can be seen more clearly by using the following notation

$(p)\alpha$ for the α-gametic vector of *Oe pratincola*
$(p)\beta$ " " β- " " " " "
$(n)\alpha$ " " α- " " " " *numismatica*
$(n)\beta$ " " β- " " " " "

The cross *Oe pratincola* × *Oe numismatica* then resolves itself into

$$(p)\alpha \times (n)\beta = \mathbf{c}\ (p)\alpha\ (n)\beta \sin\theta = Oe\ \ pratincola,$$

with the reciprocal cross given by

$$(n)\alpha \times (p)\beta = -\mathbf{c}\ (n)\alpha\ (p)\beta \sin\theta = Oe\ \ numismatica,$$

instead of

$$\mathbf{p} \times \mathbf{n} = \mathbf{c}\ pn \sin\theta,$$

and

$$\mathbf{n} \times \mathbf{p} = -\mathbf{c}\ np \sin\theta,$$

respectively, which will be discarded in favor of the more exact relations The diagram of Figure 18, then, will be replaced by

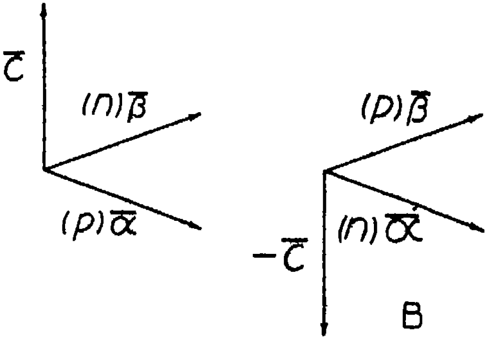

Fig 20

the more elucidative one of Figure 20 *A*, in which the conventional position of the vectors shows that the female parent was *Oe* *pratincola* and contributed the α-gamete, that the male parent was *Oe numismatica* and contributed the β-gamete, and that the cross is matroclinic (patroclinic inheritance would have the cross product vector with downward sense, but with a positive sign) Figure 20 *B* would replace Figure 19

SOME COMPLICATIONS OF THE GENETICAL RESULTS

VIII

It has been seen that *Oe pratincola* × *Oe numismatica* = modified *Oe pratincola*, which is true except when large progenies are grown, when a few plants of *Oe numismatica* are observed as well as a very few other plants neither *Oe pratincola* nor *Oe numismatica*, but which divide themselves into two distinguishable groups Likewise, the reciprocal cross shows a few plants of *Oe pratincola* and the other two unnamed groups just mentioned

The crosses thus far considered have been such that the progeny had the gametic constitution $\alpha\beta$ or $\beta\alpha$ This in general is the case, although a few plants can have both egg and sperm containing the α- or β-gametes forming such combinations upon fertilization as $\alpha\alpha$ or $\beta\beta$ in addition to the usual forms This leads to a complication which, however, still fits into the vector scheme here proposed Under the alpha-beta hypothesis it may be said that a few eggs are formed with β-gametes and that upon fertilization an occasional union of a sperm with an egg of like gametic constitution takes place Hence the cross becomes

$$\textit{Oe pratincola} \times \textit{Oe numismatica} \begin{cases} \alpha\beta \text{ many } (\textit{pratincola}) \\ \beta\alpha \text{ few } (\textit{numismatica}) \\ \alpha\alpha \text{ very few} \\ \beta \text{ very few} \end{cases}$$

with the reciprocal cross similar

Dr Blanchard[18] says, in recording her work on mutations of *Oe pratincola* "It is the alpha gametes which are responsible for the form of the plant, except so far as the four known beta factors may modify it Therefore alpha-alpha hybrids have the combined appearance of the two forms represented Any alpha-alpha plant has a characteristic appearance which is easily recognizable On closer examinations the characters of the two parent forms can be distinguished, and, at least in many cases, the parentage can be determined without help from the records " The beta-beta plants are marked by a characteristic gray aspect, due to the pubescence, and are very frequently sterile dwarfs that seldom flower and therefore are easily distinguishable from the alpha-alpha plants or either f *typica*

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[18] Blanchard, Frieda Cobb, "Heterogametic and Homogametic Hybrids between Two Mutations of *Oenothera pratincola*,' *Pap Mich Acad Sci, Arts and Letters*, 6 133–180 1926. Quotation on page 141

IX

For the vector explanation consider the vectors

$$\mathbf{p} = (p)\alpha + (p)\beta$$

and

$$\mathbf{n} = (n)\alpha + (n)\beta$$

Then the cross *Oe pratincola* × *Oe numismatica* would be given in full by

$$[(p)\alpha + (p)\beta] \times [(n)\alpha + (n)\beta]^{14} =$$
$$(p)\alpha \times (n)\alpha + (p)\alpha \times (n)\beta + (p)\beta \times (n)\alpha + (p)\beta \times (n)\beta,$$

in which

$$(p)\alpha \times (n)\beta = \mathbf{c}\ (p)\alpha(n)\beta \sin\theta$$

has been called *Oe pratincola*, so that

$$(p)\beta \times (n)\alpha = -\mathbf{c}\ (p)\beta(n)\alpha \sin\theta = -(n)\alpha \times (p)\beta$$

is *Oe numismatica*, and the other two combinations

$$(p)\alpha \times (n)\ \alpha = \mathbf{c}'\ (p)\alpha(n)\alpha \sin\theta'$$
$$(p)\beta \times (n)\beta = -\mathbf{c}'\ (p)\beta(n)\beta \sin\theta'$$

will be neither *Oe pratincola* nor *Oe numismatica*, but will be distinguishable from each other

The diagram would now be somewhat more complicated, as

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[14] The vector cross product is distributive, except that the order of the factors must be carefully maintained upon expansion

Figure 21 shows The vector **p** and the vector **n** are in the plane of the paper, while $(p)\alpha$, $(p)\beta$, $(n)\alpha$ and $(n)\beta$ must be visualized as extending above or below the plane of the paper In this $(p)\alpha$ and $(n)\beta$ determine the plane to which **c** is normal, while $(p)\alpha$ and $(n)\alpha$ determine the plane to which **c′** is normal Consequently **c** and **c′** will not be parallel, so that **c′** will be unable to represent

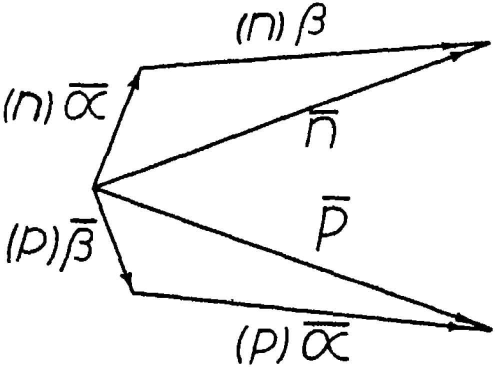
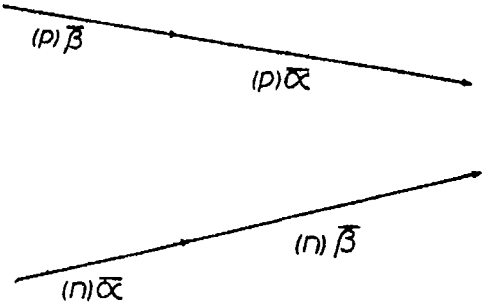


Fig 21

either *Oe pratincola* or *Oe numismatica*, but will represent a characteristic plant The vector −**c′** holds the same relation to **c′** that −**c** does to **c**

It will be found more convenient, however, to project $(p)\alpha$ and $(p)\beta$ upon **p** and $(n)\alpha$ and $(n)\beta$ upon **n** in order to have all parental vectors in the same plane Then, since many more eggs have α- than β-gametes, the pistillate vector will be represented by Figure 22 The functioning sperm vector will then have a like ratio of β to α, as shown by Figure 22*B*

If, then, the complete result of the cross *Oe pratincola* × *Oe numismatica* is represented diagrammatically, Figure 23 would result Here **c′** should not be represented as parallel to **c** since the alpha-alpha or beta-beta plants are not like either f *typica*, but a diagram representing all details would be complicated to



B

Fig 22

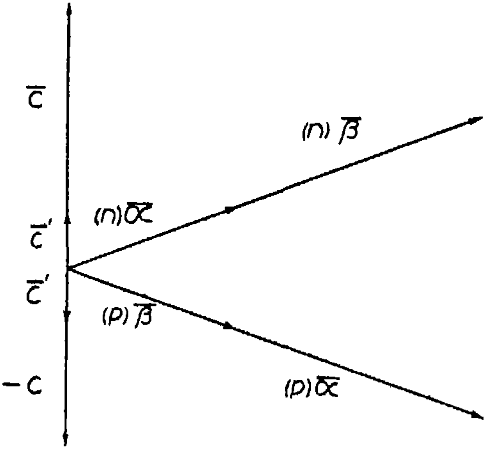


Fig 23

draw and hard to visualize Figure 23 may be separated into its various components as given in Figures 24 *A*, *B*, *C* and *D*, which shows from which parent each gamete came and the way it was combined with others to form a plant of *Oe pratincola*, *Oe numis-*

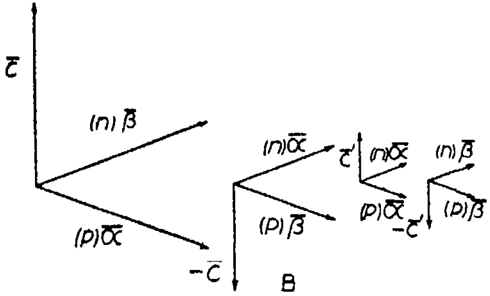


FIG 24

matica, alpha-alpha form or beta-beta form, respectively, in the cross under consideration

The reciprocal cross would have complementary parts, i e the *p*'s and the *n*'s would be interchanged and the cross product vectors would all be reversed in sense

While working with *Oe Reynoldsii*, one of the wild species of Oenothera that has undergone mutation, La Rue and Bartlett [18] found further variation in matroclinic inheritance that may be considered as a special case of the results given in the previous paragraph They studied the three mutations of *Oe Reynoldsii* named and characterized by Bartlett as

mut. semialta, about half as high as f typica
mut debilis, a weak dwarf with much reduced foliage
mut bilonga, closely resembling mut *semialta* in form and stature, but with fruit twice as long

In cultures there were no gradations between these mutations, each being so distinct as to be easily recognized

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[18] La Rue, Carl D, and Bartlett, H H, "Matroclinic Inheritance in Mutation Crosses of *Oenothera Reynoldsii*," *Am Journ Bot*, 4 119-144 March, 1917

The value here is in the result of crosses which are as follows

typica × semialta → typica →
typica × debilis → typica →
typica × bilonga → typica + yellow twin → typica →
semialta × bilonga → semialta →
debilis × typica → debilis →
debilis × semialta → debilis →
debilis × bilonga → ½ debilis + ½ bilonga
bilonga × typica → bilonga + yellow twin → bilonga →
bilonga × semialta → bilonga + yellow twin → bilonga →

With one exception (*debilis* × *bilonga*) the inheritance is strictly matroclinic, as the yellow twin never develops into a plant, but dies soon after the cotyledons are pushed through the ground

XI

In this case it must be that the eggs are formed in such a way that one half of them contain α-gametes and the other half contain β-gametes This would lead to a vector composed of α and β portions of equal length in contrast to the vector of *Oe pratincola* given in Figure 22, in which there is a great difference in the lengths of the α and β portions To keep the language of this paper, the cross would be

$$[(d)\alpha + (d)\beta] \times [(b)\alpha +$$
$$(d)\alpha \times (b)\alpha + (d)\alpha \times (b)\beta + (d)\beta \times (b)\alpha + (d)\beta \times (b)\beta,$$

of which

$$(d)\alpha \times (b)\alpha \text{ and } (d)\beta \times (b)\beta$$

very seldom occur, while

$$(d)\alpha \times (b)\beta = \mathbf{c}\ (d)\alpha(b)\beta \sin\theta = \textit{debilis}$$

and

$$(d)\beta \times (b)\alpha = -\mathbf{c}\ (d)\beta(b)\alpha \sin\theta = \textit{bilonga}$$

occur in equal numbers.

This cross would then be represented by Figure 25 (leaving out the insignificant component of composition $\alpha\alpha$ or $\beta\beta$) It will be noticed that the force **c** is balanced by the force $-\mathbf{c}$, with the

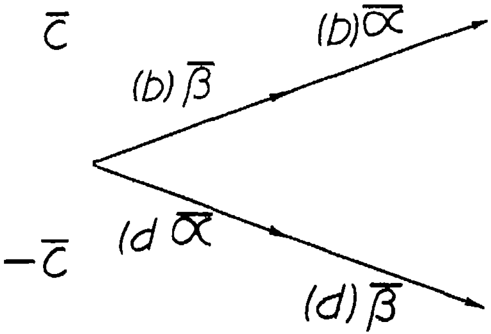

Fig 25

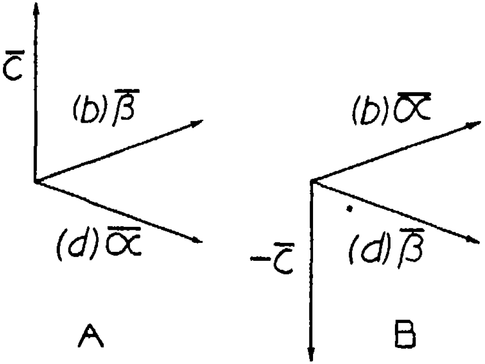

Fig 26

result that in this cross there is no advance in numbers of either type of plant over that of the other Figure 25 may be split into Figures 26 *A* and *B*, showing the constitution and formation of *Oe debilis* and *Oe bilonga*, respectively

MUTATIONS

XII

It has been observed that the mutations of *Oe Reynoldsii* are all plants of lesser stature than that of f *typica*, but no adequate explanation of the reason for this has been given Also it might be added that the mutations are less hardy than f *typica*, being much more difficult to grow in the garden and probably very seldom existing in the wild state Since this weakness of mutated forms seems to be universal, it should be possible for the vector formulation of Oenothera behavior to take it into account With this in mind we may analyze more carefully the laws proposed here

Although it has not been previously pointed out, it has been tacitly assumed that the pistillate vector and the functioning sperm vector are of the same length, since every egg must be fertilized by one and only one sperm Therefore, for this work it might be said that instead of

$$\mathbf{a} \times \mathbf{b} = \mathbf{c}\, ab \sin \theta,$$

the simpler relation

$$\mathbf{a} \times \mathbf{b} = \mathbf{c}\, a^2 \sin \theta$$

might be used and the parallelogram multiplying the vector **c** is an equilateral parallelogram as it has been pictured in the figures Then, since the vector **c** gives only direction and a is always constant, nothing can change vectorially under mutation except the angle θ If, then, hardiness of a plant, or, more broadly, the ability to persist and reproduce is considered as determined by the area of the base parallelogram, a good mathematical analogy is obtained If f *typica* were invariably the most hardy plant, its parallelogram would have a maximum area and so would be a square and θ would be 90° The non-mutation inheritance would then be given by

$$\mathbf{a} \times \mathbf{b} = \mathbf{c}\, ab \sin 90^\circ = \mathbf{c}\, a^2$$

Since most mutations tend to decrease the hardiness of the plant, the angle θ will either decrease or increase from 90°, since

$$0 \leq \sin\theta < 1 \text{ for } 0 \leq \theta < 90^\circ \text{ or } 90^\circ < \theta \leq 180^\circ$$

The most vigorous chromosome combination would theoretically be the f *typica*, with $\theta = 90^\circ$ If, however, a rare mutation were to occur, more vigorous than f *typica*, it would indicate that θ had not been 90°, but perhaps close to it If θ were close to 90°, nearly all mutations would be weaker than the parent

From this standpoint there are some interesting implications as to hybridization If a new form were created by the fusion of an α-gamete with a different β-gamete (from a somewhat distantly related species group), a new combination would be created in which θ might be much less than 90° and there would then be a possibility of many mutations from the hybrid parent stronger than the parent itself

For mut *semialta*, then, the equation

$$\frac{ab}{2} = ab\sin\theta$$

for a relative determination of its hardiness must be solved Here

$$\tfrac{1}{2} = \sin\theta \qquad \theta = \sin^{-1}\tfrac{1}{2}$$

so

$$\theta = 30^\circ$$

Likewise for mut *debilis*

$$\theta = 14^\circ\,30'$$

XIII

A very good reason for the decrease in angle can be seen by considering the inverse process to cross multiplication The entire explanation so far has been considering the process of taking two vectors **a** and **b**, or say $(p)\alpha$ and $(p)\beta$, and forming their cross product to obtain

$$\mathbf{c}\ (p)\alpha\ (p)\beta\ \sin\theta,$$

which was defined as *Oe pratincola* With the $(p)\alpha$ and $(p)\beta$ determined, there will be a unique result This process of combining two vectors in cross multiplication to form a third vector corresponds to fertilization in which the elements of two individuals are united to form a third individual Now start with

$$c\ (p)\alpha(p)\beta \sin \theta$$

and decompose it into $(p)\alpha$ and $(p)\beta$ It will be seen that this can be done in only one way since the sides of the base parallelogram must remain constant This process of splitting a vector into two vectors whose cross product is the original corresponds to the reduction division in which the parent forms two elements such that, if two elements of this kind are properly combined, an individual indentical with the first will be formed If, however, as this decomposition takes place, the angle between the vectors $(p)\alpha$ and $(p)\beta$ is changed from that of f *typica*, thus forming new vectors $(p)\alpha'$ and $(p)\beta'$, a mutation will have occurred without altering the magnitudes of the vectors or changing the chromosomes in any way This could be done in an infinite number of ways, so that theoretically there could be an infinite number of mutations

If only the laws of chance were involved, plants of every gradation of hardiness from a non-developing seed to the sturdy f *typica* would be formed and the 90° angle would not be formed any more times than any other named angle, whereas f *typica* is known to occur many more times than any other type Also, the 30° angle of mut *semialta* and the 14° 30′ angle of mut *debilis* occur more than any other except the 90° angle in *Oe Reynoldsii* It must, therefore, be assumed that within the plant there is some force that influences the gametes to form vectors of only a few definite directions, thus resulting in relatively few types of plants This is given because it strengthens the notion that many of the Oenothera phenomena possess direction, but that there is little left to chance, which is a ruling factor in Mendelian inheritance

XIV

SUMMARY

In conclusion we may consider this point of view of the analogy in the proof of Oenothera genetics with that of the better established Mendelian branch of genetics

Proof of Mendelian laws	*Proof of Oenothera laws*
1 Hypothesis of a physical basis for each character, with each carrier having an allelomorph and several carriers linked together with independent segregation of these linked groups	1 The alpha-beta hypothesis of Bartlett in which there are no allelomorphic pairs and the results of inheritance are restricted through limitation of free chromosome segregation
2 Cytological discovery of the paired chromosomes with behavior that parallels the hypothetical linked group of mechanical carriers	2 Cytological discovery of a chain formation of chromosomes with definite organisations that parallel the alpha-beta hypothesis
3 Scalar mathematics especially the laws of chance as a basis for the explanation of the combinations of characters and simple algebra as a means of formulating the results	3 The vector cross product as an explanation of directed inheritance and the vector analysis notation as a means of formulating the results

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PETUNIA PARODII, A NEW SPECIES OF THE SUBGENUS PSEUDONICOTIANA FROM ARGENTINA *

WILLIAM C. STEERE

Petunia Parodii, sp. nov. Herbacea, erecta, ramosa, dense viscido-pubescens. Caules 5-8 dm. longi, internodiis 5-8 cm. longis. Folia ovata, integerrima, apice acuta vel subacuta. Pedicelli floriferi 3.5-7 cm. longi, fructiferi, 6-9 cm. longi. Calyx campanulatus, laciniis lineari-oblongis vel spatulatis, 8-15 mm. longis. Corolla alba, infundibuliformis, tubo cylindrico, 5-7.5 cm. longo, 1-3 mm. in diametro, limbo 4.5 cm. in diametro, purpureo-venoso, lobis acutis. Stamina 5, usque ad media corollae tubo adnata, 4 aequilonga, vel paululo inaequalia (vix didynamia), 6-7.5 cm. longa, quintum parvius, 5-6.5 cm. longum. Stylus filiformis. Capsulae 12-15 mm. longae, in diametro 6-10 mm., apice bifidae. Semina 21-28 diebus post anthesin maturantia, minute reticulato-aspera. *P. Parodii* differt a speciebus affinibus subgeneris Pseudonicotianae statura majore erecta, internodiis longioribus, tubo corollae praesertim longiore, lobis acutioribus minoribus, purpureo-venoso, staminibus 4 subaequilongis, non (modo *P. axillaris* (Lam.) BSP.) valde didynamis. Specimen typicum ex seminibus a cl. Dr. Lorenzo R. Parodii in provincia Formosa, Argentina, Feb., 1928, lectis, in Horto Botanico Universitatis Michiganensis cultum anno 1929 sub num. W. C. S. 202-1.

Plants erect, branching, stout for the genus, densely glandular-pubescent, the viscid hairs about 1 mm. in length. *Stems* green, diffusely branched, erect or somewhat decumbent at the base, herbaceous to slightly suffrutescent, 5-8 dm. high, internodes 5-8 cm. long. *Leaves* soft, fleshy, entire, apex acute to subacute, the basal 2-4 cm. long, 1.5-3 cm. wide, narrowed into short, margined, distinct petioles, alternate, ovate to broadly oval, the uppermost smaller, elliptical to lanceolate, subsessile, those sub-

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* Paper from the Department of Botany of the University of Michigan, No. 320.

tending the flowers opposite, sessile, cordate-clasping, the lower 2–5 cm wide, 1 5–4 cm long, the upper minute *Peduncles* slender, hirsute, at flowering time 3 5 7 cm long, in fruit, 6 9 cm long *Flowers* large, solitary on axillary or terminal peduncles *Calyx* campanulate, glandular pubescent, deeply cleft or parted into 5 narrowly linear-oblong to spatulate unequal segments, 8–15 mm long, the tubular basal portion somewhat angled, 3–7 mm long *Corolla* funnel shaped, white, seated loosely in the calyx, the tube straight, cylindric, slightly enlarged above, densely pubescent, deeply veined with purple, 1 3 mm in diameter, 5-7 5 cm long, the limb plicate, purple-veined 4–5 cm in diameter, normally five lobed, the lobes rather pointed *Stamens* 5, perfect, inserted slightly above the middle of the corolla, and included in it, 4 of them of equal length or very slightly didynamous 6 7 5 cm in length, the fifth distinctly smaller, 5-6 5 cm long, filaments slender, glabrous, anthers ovoid, two-lobed *Pistil* Ovary two-celled, ovate, style filiform, 5-7 5 mm long stigma a green, dilated, bilobed disc Capsule ovoid, acute, 6-10 mm in diameter, 12–15 mm long, two-celled, two-valved, each valve slightly cleft at the tip Seeds small, numerous, brown, testa reticulate roughened with minute thickenings, ripening 3 4 weeks after pollination ARGENTINA central part of the province of Formosa, *L R Parodi* February, 1928 cultivated at Botanical Garden, Univ Mich under no W C S 202 1 (Type specimen from cultivated plant in Herb Univ Mich , *leg* W C Steere)

Petunia Parodii, sp nov (see Pl XXXII), resembles *P axillaris* (Lam) BSP (see Pl XXXIII) in several ways and obviously belongs with it in the subgenus Pseudonicotiana R E Fries This affinity is shown by leaf shape and manner of branching, by the white corolla, with its subcylindric tube and median attachment of the filaments, and also by the shape of the fruits It was determined by a cytological investigation that there are 14 diploid chromosomes, which are completely paired and appear as 7 gemini at diakinesis during microsporogenesis This is also the number found in *P axillaris* (Lam) BSP

Despite the similarities, *P Parodii* may easily be distinguished from its allies by the larger, more erect stems, with longer inter-

Habit of *Lelania Larodii* W. C. Steere sp. nov.

PLATE XXXIII

Habit of *Petunia axillaris* (Lam.) BSP × 1

PLATE XXXIV

Comparison of corolla limb of *P. parodii*, sp. nov. (top) with that of *P. axillaris* (Lam.) BSP.

nodes, which give a characteristic habit to the plant, by the unusually long corolla tube, the smaller limb, with more pointed lobes, and the presence of the deep purple veining (see Pl XXXIV) The stamens also are distinctive, because of the very small difference among the 4 long stamens, which are strongly didynamous in *P axillaris* (Lam) BSP The time required for ripening of the seed after pollination is only 3–4 weeks, considerably shorter than that in any other Petunia in the writer's cultures at the Botanical Garden at Ann Arbor

Seed of this species was very kindly sent to me by Dr Lorenzo R Parodi, professor of botany in the University of Buenos Aires, Argentina, who collected it in the central part of the province of Formosa during February, 1928 It was sent for *P axillaris* (Lam) BSP , though Dr Parodi mentioned the fact that it was somewhat different from the strain grown at the University of Buenos Aires

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AN UNUSUAL SEASONAL GROWTH RING IN EUCALYPTUS *

WALTER W TUPPER

WHILE the writer was working at the Yale Forestry School, his attention was called by Professor Samuel J Record, of that school, to an unusual seasonal growth-ring in the mature stem wood of Eucalyptus This unusual wood came from the so-called alpine or mountain "ash," *Eucalyptus delegatensis* R T Baker, which grows in snow country, high up on the southern table lands in the Australasian region The wood structure of this species has been carefully described, with photomicrographic illustrations, by Dr Welch [1] of the Technological Museum, Sydney, Australia Dr Welch found that this species was the nearest approach to a ring-porous timber in the eucalypts, and that the pores were occasionally entirely absent in the late wood In every case, Dr Welch writes to me, there is a reduction in pore size and pore count in the late wood In the specimen of wood which the writer found to be so unusual and interesting the vessels are almost entirely absent in the early or spring wood, while large and conspicuous vessels are clustered together in the late fall wood, as is shown in the accompanying photomicrograph (Pl XXXV)

The end of the late wood has a much sharper and more even line than does the transition from the early wood to the later formed part This fact, which is quite evident from the photomicrograph (Pl XXXV), together with the curvature of the annual rings and the number of rays, shows that the large and numerous vessels are in the late or fall wood in the unusual specimen, instead of in the early or spring growth, as has been supposed

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* Paper from the Department of Botany of the University of Michigan, No 332

[1] Welch M B 'The Wood Structure of Certain Eucalypts belonging Chiefly to the 'Ash Group,'' *Journ and Proc Roy Soc New South Wales* Vol 60, 1927

The ring-porous type of wood, which Dr Welch supposed this eucalyptus to have, is quite common in such trees as the chestnut, and has so very much larger and more numerous vessels in the spring wood than in the summer wood that distinct rings of pores are clearly evident even without any magnification In several plants having ring-porous wood, such as the oak, it has been observed that if the tree is defoliated by insects, or by any other agency in the early summer, and puts out a second crop of leaves later that same season, the wood for that year will have a second zone of large, numerous vessels, similar to that which occurs normally only in the first part of the season's growth So far as the writer is aware, however, there is no record of a wood having large, numerous and conspicuous vessels in the late summer or fall wood, and either no vessels at all or exceedingly few and very small ones in the earlier part of the same season's growth

The writer[1] has called attention to the widest possible variation in these characters in the woods of the Lauraceae from the sharply ring-porous type of Sassafras to the type found in Cinnamomum, in which no annual rings at all are evident and in which the vessels are evenly distributed throughout the wood Although certain families of woody plants have clearly defined tendencies toward ring-porous or diffuse-porous woods, and even toward characteristic arrangements of the vessels, which are constant and striking enough to be of great value as diagnostic characters in the identification of their woods, yet other families exhibit such a variation in the size and distribution of the vessels, depending upon the rate of growth, the time that the new leaves are formed, and upon other physiological activities of the individual plants, that they are almost valueless for purposes of identification

The unusual structure of this Eucalyptus wood seems to be due to the retardation in the normal formation of new leaves and shoots for a considerable time after the activity of the cambium

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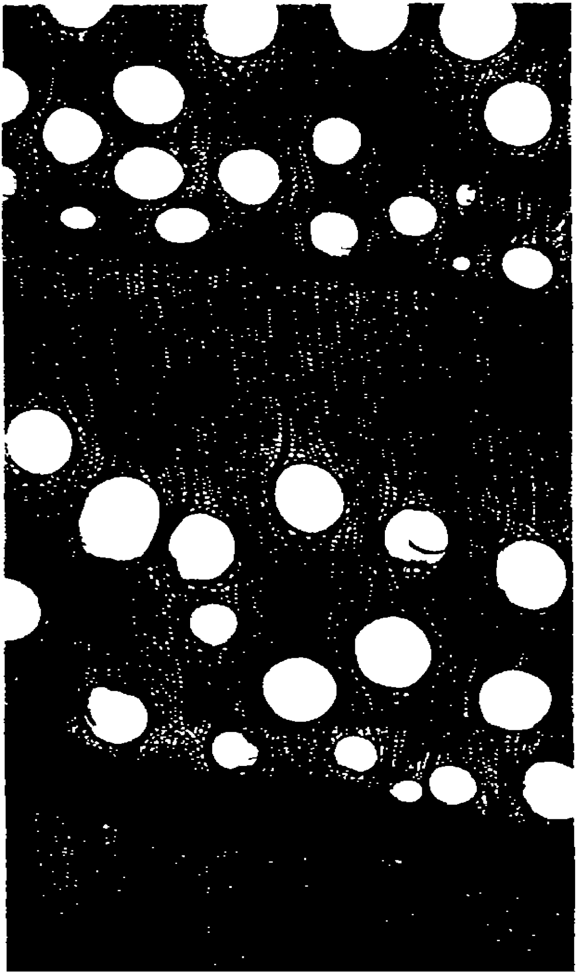
[1] Tupper, Walter W, "A Comparative Study of Lauraceous Woods,' *Am. Journ Bot*, 14 (No 9) 520-525 November, 1927

PLATE XXXV



started for that season This retardation may have been caused by extreme cold, drought, wind, or by some other external condition which might easily be operative in the high altitudes at which this species grows

University of Michigan

EXPLANATION OF PLATE XXXV

A photomicrograph of the mature stem wood in transverse section of *Eucalyptus delegatensis* R T Baker, showing the large and conspicuous vessels clustered together in the late or fall wood and the almost complete absence of any vessels at all in the early or spring growth The clear and sharp line of demarkation between the last fall wood and that of the first wood formed in the spring as well as the curvature of the rings (not shown), indicates which is the fall and which the spring growth.

MORPHOLOGICAL STUDIES ON THE SEED OF *MESEMBRIANTHEMUM CRYSTALLINUM* L

EDWARD F WOODCOCK

THE curved embryo has been considered by Engler and Prantl (4) a character of sufficient importance and limited occurrence to warrant the arrangement of plants with such an embryo as the Order Caryophyllales or Centrospermae The results of the serum diagnostic investigations of Malligson (7) show a grouping of the families very similar to that of Engler and Prantl

The prevalence of the curved type of embryo in the Caryophyllales has also been observed by several recent investigators in their studies of seed morphology in this Order Artschwager (1) observed the curved embryo of *Beta vulgaris* L to have over the radicle a cap of endosperm, the cells of which are filled with dense granular material The storage material outside the embryo is starchy perisperm

The writer has found a somewhat similar arrangement of the embryo, endosperm and perisperm in the Caryophyllaceae (13,14) In his studies on the Polygonaceae (9,10), Phytolaccaceae (11), Portulacaceae (12), Nyctaginaceae (15) and Cynocrambaceae (16), the curved embryo has been observed to be a prominent character All the foregoing families have perisperm as the storage tissue except the Polygonaceae and the Cynocrambaceae, which have endosperm In the Polygonaceae a portion of the endosperm is of a protein nature The presence of endosperm as a storage tissue in this family has been observed by Stevens also (8) The writer has observed a crushed cap of endosperm tissue over the radicle in the Nyctaginaceae and a sheath of crushed endosperm entirely surrounding the embryo in the Portulacaceae

The results of the recent investigations of the seed morphology in the Centrospermae by the writer and others have assisted in the interpretation of the terms "albumen" as used in such floras as that of Britton and Brown (3), and "endosperm" as used by Bentham and Hooker (2) and Harz (6)

The present paper has to do with the seed morphology in *Mesembrianthemum crystallinum* L, a member of the Aizoaceae and another representative of the Order Caryophyllales

DESCRIPTION AND DISCUSSION OF THE MORPHOLOGY OF THE SEED

The various stages of seed development were studied by means of microtome sections stained in Delafield's hematoxylin

The five-loculed, compound pistil has axial placentation and several ovules in each locule The slender funiculus of each ovule equals in length that of the ovule itself (Pl XXXVI, Fig 1) The campylotropous ovules are rounded in outline when observed from the side and the chalazal region appears somewhat flattened (Fig 2) In cross-section the outline of an ovule is slipper-shaped (Fig 4) and the micropylar portion is somewhat narrower than the chalazal portion

Each of the two integuments is composed of two layers of flattened cells (Fig 2) The surface of the ovule is rough, owing to the dome-shaped, outer tangential wall of each of the epidermal cells The writer has observed in earlier investigations that, instead of one cell being concerned, two or three cells go into the formation of similar elevations on the surface of the ovule of *Cerastium vulgatum* L and *Claytonia virginica* L The projecting rim of the inner integument is somewhat reflexed upon that of the outer integument The young embryo sac is separated from the micropyle by several layers of nucellus cells and its most rapid enlargement is along the axis of the ovule The disorganization of the central part of the nucellus by the embryo sac is along a region characterized by somewhat elongated, large parenchyma cells, which merge into a chalazal region of smaller, isodiametric parenchyma cells In the nucellus between the embryo sac and the micropyle there is a narrow region of elongated cells extending from the micropyle to the embryo sac This region of cells becomes disorganized to form a canal through which the pollen tube enters This canal retains its form as further seed development occurs (Fig 5)

The writer made no observation of the embryo sac before the quadrant stage of the embryo Guignard (5) has observed that the embryo sac in this genus has the typical eight-nucleate condition at the time of fertilization At the quadrant stage (Figs 1, 5) the embryo sac has proceeded along the median line of the ovule and the fertilized egg has given rise to a row of cells consisting of a short, few-celled suspensor and the quadrant stage of the embryo The free nuclear endosperm completely lines the embryo sac and surrounds the embryo and suspensor The canal, through which the pollen tube reached the embryo sac, is evident and is lined with broken down cell-remains

As growth proceeds the embryo sac elongates and broadens (Pl XXXVII, Fig 7) In longitudinal section the sac is curved in outline The chalazal end of the sac often has pseudopodium-like extensions into the nucellus Transverse divisions occur in the suspensor, producing a row of cells, some of which may later divide longitudinally (Pl XXXVI, Fig 3) All the cells except two or three next to the embryo become broadened In the stage shown in Plate XXXVII, Figure 7, the micropylar portion of the endosperm has become cellular, thus partially filling the embryo sac By the time the embryo is ready to produce its cotyledon and plumule primordia (Pl XXXVI, Fig 3) the embryo sac is almost completely filled with cellular endosperm, each cell of which is thin-walled and much vacuolated Most of the endosperm cells have only one nucleus, but occasionally two nuclei are evident (Pl XXXVII, Fig 8)

As the embryo dissolves its way through the cellular endosperm, which very soon completely fills the embryo sac, it becomes differentiated into radicle, hypocotyl and two cotyledons At the stage shown in Figure 6 the embryo has proceeded about halfway down the embryo sac and has become slightly curved At this stage numerous, compound starch grains, which are in the shape of a flattened ellipsoid, are evident in each cell of the nucellus (Figs 9, 13) There is no indication of storage material in the cellular endosperm in this stage (Fig 8) or in later stages

As the seed comes to maturity there is evident a marked change in the epidermal layer of the outer integument The outer tangential, dome-shaped wall of each cell is much thickened, and the inner surface is often corrugated A prominent, spiny deposit of cutin occurs on the outer surface of the wall (Fig 10) The radial and inner tangential walls remain thin and uncutinized The radicle of the embryo has a cap of endosperm, one or two cells in thickness The cells of this cap are filled with dense, granular contents The remaining part of the cellular endosperm, which earlier filled the embryo sac, has completely disappeared The radicle, hypocotyl and cotyledons are nearly equal in diameter Each cotyledon is semicircular in outline when seen in cross-section, with its flat surface nearly at right angles to the flattened sides of the seed (Fig 12) At the base of the cotyledons there is evident the plumule in the form of a small, conical elevation The cells of the perisperm are filled with closely packed, compound starch grains, which have lost their flattened, ellipsoidal form and have become somewhat angular

SUMMARY AND CONCLUSIONS

The ovule of *Mesembrianthemum crystallinum* L is campylotropous, somewhat flattened, and appears slipper-shaped in outline when cut in cross-section The pollen tube reaches the embryo sac by passing through a canal formed in the nucellus between the embryo sac and the micropyle The curved embryo lies to one side of the seed and the radicle has a cap of cellular endosperm, whose cells are filled with dense, granular contents The major portion of the storage tissue is starchy perisperm The outer wall of the testa epidermis is much thickened and cutinized

The seed morphology of this representative of the Aizoaceae shows marked similarity to that of other families already investigated and aids in establishing, on a morphological basis, the close relationship existing between the families in the Order Caryophyllales

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EXPLANATION OF PLATES XXXVI–XXXVII

Seed of *Mesembryanthemum crystallinum* L

All figures drawn with aid of camera lucida The following abbreviations are used C, cotyledons, CA, canal, CH, chalaza, CU, cuticle, E, embryo, EN, endosperm, ES, embryo sac, F, funiculus, H, hypocotyl, IN, inner integument, M, micropyll, N, nucellus, ON, outer integument, OW, seed coat (testa), P, perisperm, PL, plumule, R, radicle, S suspensor, ST, starch grains

PLATE XXXVI

Fig 1 Longitudinal section of young ovule, showing long slender funiculus (× 75)

Fig 2 Detail of longitudinal section through young ovule (× 207)

Fig 3 Suspensor and embryo (× 207)

Fig 4. Cross-section of young ovule in plane indicated by broken line in Figure 2 (× 207)

Fig 5 Detail of micropylar portion of young ovule, with embryo in the quadrant stage Canal evident between micropyle and embryo sac (× 207)

PLATE XXXVII

Fig 6 Longitudinal section through ovule at the time the cotyledons are well developed in the embryo and the embryo sac is completely filled with cellular endosperm (× 75)

Fig 7 Longitudinal section through ovule at the stage in which cellular endosperm has appeared only in the micropylar portion of the embryo sac (× 75)

Fig 8 Endosperm cells showing vacuolated condition (× 430)

Fig 9 Cells of nucellus with numerous flattened, ellipsoidal starch grains (× 430)

Fig 10. Epidermis of mature seed with spiny cuticle (× 430)

Fig 11 Longitudinal section of mature seed, showing testa, curved embryo with cap of endosperm, and perisperm (× 75)

Fig 12 Cross-section of mature seed in plane indicated by broken line in Figure 11 (× 75)

Fig. 13 Single compound starch grain (× 1700)

PLATE XXXVI

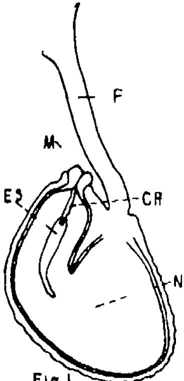

Fig 1

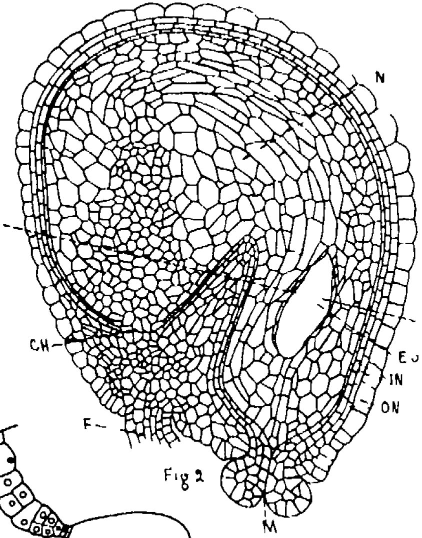

Fig 2

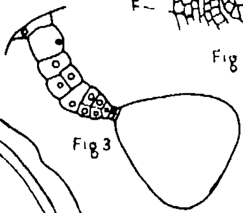

Fig 3

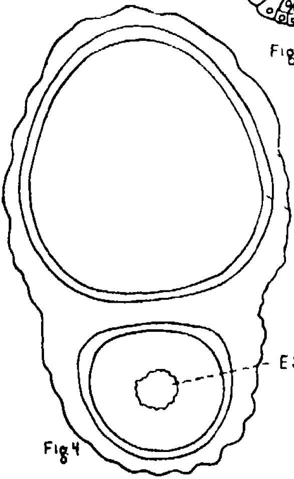

Fig 4

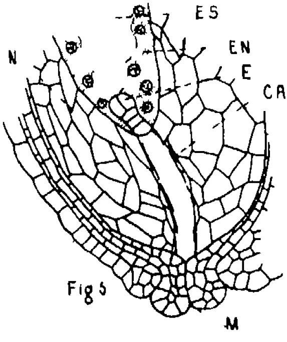

Fig 5

PLATE XXXVII

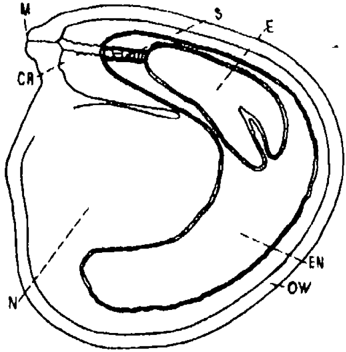

Fig 6

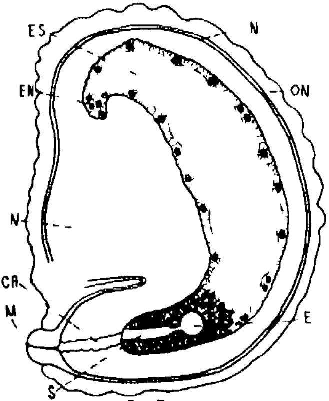

Fig 7

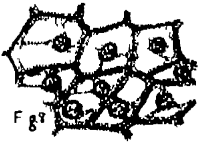

Fig 8

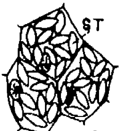

Fig 9

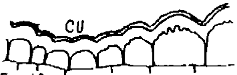

Fig 10

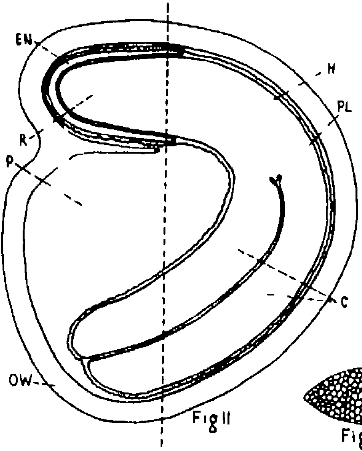

Fig 11

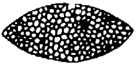

Fig 13

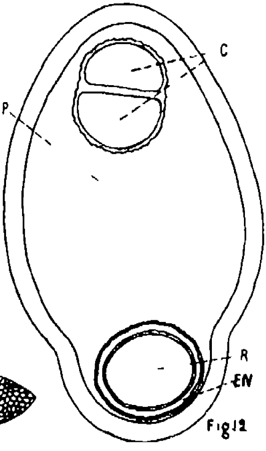

Fig 12

THE DISTRIBUTION OF INTERFERENCE IN THE X-CHROMOSOME OF DROSOPHILA *

ERNEST G ANDERSON AND MARCUS M RHOADES

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INTRODUCTION

THE amount of interference for a given map distance is not equal for different regions of the same chromosome The problem of unequal distribution of interference has been discussed by Bridges and Morgan (1923) and later by Morgan, Bridges and Sturtevant (1925) The most marked differences were noted in the second and third chromosomes, where the interference is lowest around the mid-points and much higher toward both ends "The symmetrical distribution about the mid-points of chromosomes II and III is probably related to the fact that these chromosomes are Y-shaped and the spindle-fiber attachment is at the mid-point" (Morgan, Bridges and Sturtevant, p 98)

In the X-chromosome the differences were smaller, but the data showed clearly that interference is greater in the left half of the chromosome than in the regions farther to the right The more recent data available for crossing-over in the X-chromosome enable us to determine the distribution of interference much more accurately than was done from the older data

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* Paper from the Department of Botany of the University of Michigan, No 273.

DATA ON CROSSING-OVER IN THE X-CHROMOSOME

The use of the so-called "alternated X-ple" stock (*sc cv v f* × *ec* ct^6 g^2), involving the region from scute to forked, has given the best available data for crossover and interference calculations. The data used in this paper are from Bridges and Olbrycht (1926, Table V), to which are added some comparable data published by Anderson (1925, Tables III and V). These data are summarized in Table I. The computed values for crossing-over and coincidence are also given. For region 4 (*ct-v*), which is long enough to include an appreciable number of doubles, the percentage of crossing-over is corrected as indicated by Bridges and Olbrycht (1926). The coincidence values were calculated in the usual way, considering triple crossovers as two successive doubles. Thus, a 1, 2, 3 triple would be included among the 1, 2 and 2, 3 doubles, but not among the 1, 3 doubles.

The coincidence values are very low when only regions from *sc* to *ct* are included. In general, they are much higher for regions of similar length nearer the forked end. But for a closer comparison, a different measure of interference will be used.

The map positions given by these data are as follows:

Scute	0
Echinus	6.8
Crossveinless	16.5
Cut	24.0
Vermilion	39.7
Garnet	50.9
Forked	62.2

RELATION OF RECOMBINATION TO CROSSING-OVER

When a crossover takes place between two loci *A* and *B*, the genes at these loci are recombined so that gene *A* is associated with *B′*, the allelomorph of *B*, and likewise *B* is associated with *A′*. The percentage of recombination of genes for the two loci can be taken as the direct measure of crossing-over only if there are no multiple crossovers. A double crossover between *A* and *B* does not give a recombination. The true number of crossovers is greater than the number of recombinations by twice the number

TABLE I

DATA ON CROSSING-OVER IN ALTERNATED X PLE STOCK COMPILED FROM BRIDGES AND OLBRYCHT (TABLE V) AND ANDERSON (TABLES III AND V)

Region	B and O Table V	Anderson Table III	Anderson Table V	Combined data	Total cross-overs	Percentage of crossing over	Coincidence
0	9554	1885	924	12363			
1	994	167	103	1264	1818	6 8	
2	1465	287	151	1903	2614	9 7	
3	1425	263	140	1828	2254	8 4	
4	2512	504	221	3237	3950	14 8	
5	1717	353	179	2249	3027	11 2	
6	1525	280	157	1962	3033	11 3	
1–2	3	0	0	3	6		03
1 3	10	1	1	12	17		11
1 4	87	24	16	127	145		54
1 5	140	38	17	195	196		96
1 6	147	29	14	190	190		93
2 3	8	1	1	10	13		06
2 4	95	20	13	128	138		36
2–5	191	43	21	255	256		87
2–6	230	45	25	300	301		1 02
3–4	26	5	4	35	41		12
3 5	110	34	12	156	161		64
3–6	161	25	12	198	202		80
4 5	76	16	6	98	107		24
4–6	225	42	23	290	314		71
5 6	46	9	3	58	64		19
1–2 6	1	0	0	1	1		
1 3 5	2	0	0	2	2		
1–3 6	3	0	0	3	3		
1 4 5	7	0	0	7	7		
1–4–6	9	1	1	11	11		
1 5–6	1	0	0	1	1		
2–3–4	1	0	0	1	2		
2–4–5	1	0	0	1	1		
2 4–6	4	3	2	9	9		
2–5–6	1	0	0	1	1		
3–4–6	4	0	0	4	4		
3 5–6	2	0	1	3	3		
4–5–6	1	0	0	1	1		
1 2–3 4	1	0	0	1	1		
1–2–3–6	1	0	0	1	1		

of double crossovers This relation is confused by many writers, owing to an incorrect use of the term "crossing-over" for "recombination" A clear presentation of the relation between crossing-over and recombination may be found in Bridges and Morgan (1923), Morgan, Bridges and Sturtevant (1925), and especially in Bridges and Olbrycht (1926)

If double crossovers occurred at random with reference to single, i e if there were no interference, then the proportion of observed doubles for any two regions should be equal to the product of the recombination proportions for these two regions Thus, the calculated amounts of recombination for successive loci A, B and C might be represented as follows

$$\begin{aligned} m &= \text{recombination for } A \text{ and } B \\ n &= \text{recombination for } B \text{ and } C \\ m + n - 2mn &= \text{recombination for } A \text{ and } C \end{aligned}$$

In the absence of interference, this relationship must be continued down to very minute regions On this basis, Haldane (1919) has developed the formula for the relation of observable recombinations to crossovers (map distance) The formula given is

$$y = 0.5\,(1 - e^{-2x}),$$

where y is the amount of recombination, x the amount of crossing-over or map distance, and e the base of natural logarithms [1]

If interference were complete, no double crossovers would take place The percentage of recombination would then be equal to the percentage of crossing-over and might be represented by the formula

$$y = x$$

Table II gives a comparison of the observed percentages of crossing-over and recombination from Table I, together with the numerical values of the term $0.5\,(1 - e^{-2x})$ The recombination

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[1] Haldane's terminology is rather confusing as he used "crossovers" in place of "recombinations" and invented the term "centimorgan" for the unit of map distance corresponding to one per cent of crossing-over

TABLE II

RECOMBINATIONS AND PERCENTAGES OF CROSSING-OVER FROM TABLE I

Regions	Percentage of crossing-over	Percentage of recombination	$0.5\,(1 - e^{-2x})$
sc–cv	16.47	16.43	141
sc–ct	24.9	24.6	196
sc–v	39.7	36.9	274
sc–g	50.9	42.8	319
sc–f	62.2	46.4	356
ec–ct	18.1	18.0	152
ec–v	32.9	31.4	241
ec–g	44.1	38.7	293
ec–f	55.4	43.6	335
cv–v	23.2	22.8	186
cv–g	34.4	32.0	249
cv–f	45.7	39.0	300
ct–g	26.0	25.1	203
ct–f	37.3	33.6	263
v–f	22.5	22.0	181

frequencies were obtained by summing all classes in Table I which showed one or three crossovers between the given loci.

The relation of recombination to crossing-over is shown graphically in Figure 27, where the percentages of recombination are plotted against the percentages of crossing-over as abscissas. The lines of no interference ($y = 0.5\,(1 - e^{-2x})$) and of complete interference ($y = x$) are added. The observed points follow an apparently smooth curve which starts along the straight line $y = x$ and curves over toward the horizontal line which corresponds to fifty per cent of recombination.

METHOD OF CALCULATION OF INTERFERENCE VALUE

Figure 28 shows graphically the expected amounts of recombination in relation to crossing-over (map distance) for no interference ($y = 0.5\,(1 - e^{-2x})$) and for complete interference ($y = x$). The percentages of recombination are plotted as ordinates against the percentages of crossing-over (map distance) as abscissas.

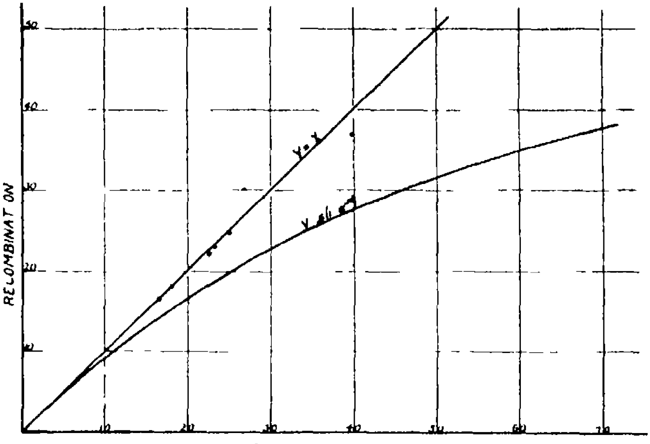


FIG 27 Relation of recombination to crossing over

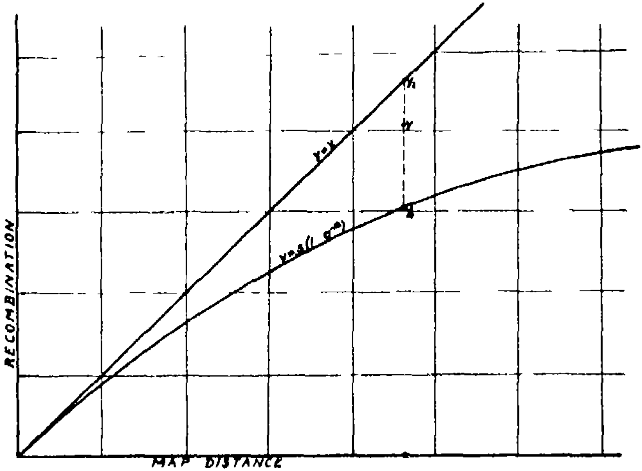


FIG 28 Diagram showing derivation of formula for interference

The observed percentage of recombinations lies between the two calculated values graphed in Figure 28 Any observed amount of recombination may be designated as y From the map distance or percentage of crossing-over (x) may be calculated the expected percentages of recombination with no interference (y_1) and with complete interference (y_2), these being the ordinates of the two lines for the given abscissa x The distance between y_2 and y_1 represents the entire range from complete interference to no interference The observed amount of interference may then be measured as the ratio of the distance between y and y_1 to the distance between y_2 and y_1, i e

$$y - y_1$$

But y_2 is equal to x and y_1 is equal to $0\ 5\ (1 - e^{-2x})$ Thus the formula becomes

$$\text{Interference value} \quad \begin{matrix} y - 0\ 5\ (1 - e^{-2x}) \\ x - 0\ 5\ (1 \end{matrix}$$

The value of this formula as a measure of interference depends to some extent on the accuracy with which the true amount of crossing-over or map distance can be determined Data on crossing-over in Drosophila have shown that for distances less than 12 units in length double crossovers are so rare that they are negligible, except for the mid-regions of chromosomes II and III Thus, *in general, for distances less than 12 units in length,* the percentage of crossing-over or map distance is essentially identical with the percentage of recombination If long distances can be broken up by shorter intervals, the percentage of crossing-over may be obtained by the commonly used method of summation of the values obtained for the shorter intervals

The computation is very simple except for the determination of the expectation for no interference, $0\ 5\ (1 - e^{-2x})$ To facilitate the use of the formula the numerical values for $0\ 5\ (1 - e^{-2}\ )$ are put in a table (Table III) for values of x from 0 11 to 1 00 (11 to 100 per cent of crossing-over) Intermediate values may be obtained by interpolation In making the calculation for interference

x	$0\ 5\ (1 - e^{-2x})$	x	$0\ 5\ (1 - e^{-})$
11	099	56	337
12	107	57	340
13	115	58	343
14	122	59	346
15	130	60	349
16	137	61	352
17	144	62	355
18	151	63	358
19	158	64	361
20	165	65	364
21	172	66	366
22	178	67	369
23	184	68	372
24	191	69	374
25	197	70	377
26	203	71	379
27	209	72	382
28	214	73	384
29	220	74	386
30	226	75	388
31	231	76	391
32	236	77	393
33	242	78	395
34	247	79	397
35	252	80	399
36	257	81	401
37	261	82	403
38	266	83	405
39	271	84	407
40	275	85	409
41	280	86	411
42	284	87	412
43	288	88	414
44	293	89	416
45	297	90	417
46	301	91	419
47	305	92	421
48	309	93	422
49	312	94	424
50	316	95	425
51	320	96	427
52	323	97	428
53	327	98	430
54	330	99	431
55	334	100	432

values, the percentages of crossing-over and of recombination should be read as hundredths. Thus, in the calculation for the *sc*–*v* region, where $x = 0.397$ and $y = 0.369$,

$$\frac{y - 0.5\,(1 - e^{-2x})}{x - 0.5\,(1 - e^{-2x})} = \frac{0.369 - 0.274}{0.397 - 0.274} = \frac{0.095}{0.123} = 0.77$$

This formula should be considered as a method of measurement and comparison only. It does not lead to any interpretation of the nature or cause of interference. For that purpose the coincidence of crossing-over (Weinstein, 1918) gives more valuable information.

DISTRIBUTION OF INTERFERENCE IN THE X-CHROMOSOME

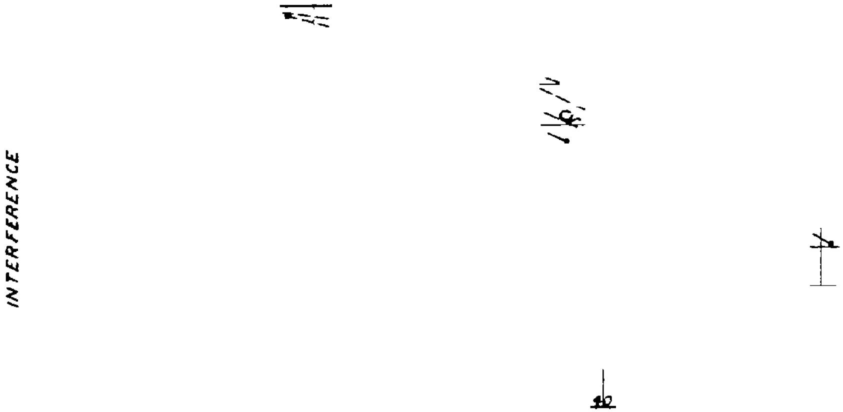
Interference values for the X-chromosome may be determined from the data presented in Table III. Table IV gives the map length and interference value for each region covered by the data.

TABLE IV

Map Distances and Interference Values

Regions	Map distance	Interference
sc–*cv*	16.5	98
sc–*ct*	24.9	94
sc–*v*	39.7	77
sc–*g*	50.0	57
sc–*f*	62.2	41
ec–*ct*	18.1	96
ec–*v*	32.9	83
ec–*g*	44.1	64
ec–*f*	55.4	41
cv–*v*	23.2	91
cv–*g*	34.4	75
cv–*f*	45.7	57
ct–*g*	26.0	84
ct–*f*	37.3	66
v–*f*	22.5	89

The relation between interference and map distance is shown graphically in Figure 29. Interference values are plotted as ordinates against map distances as abscissas. Regions beginning with



of un nce Dotted rved ts for
echinus, cross

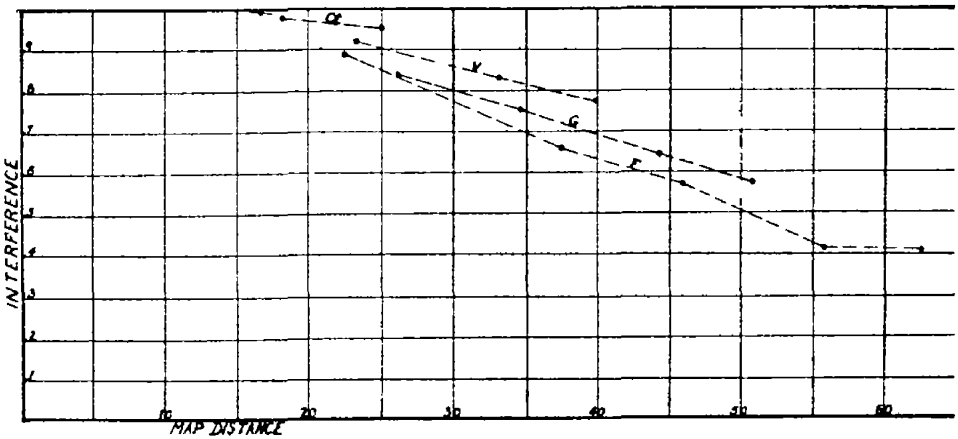


FIG 30 Relation of interference to map distance Dotted lines connect observed points for regions end

scute are connected by a dotted line. Similarly for regions beginning with echinus, crossveinless and cut. It will be noted that these form a series of successive, roughly parallel lines, with the line for scute being highest, followed successively by those for echinus, crossveinless and cut in their respective map order. This shows that for corresponding map distances the interference is greater for regions toward the left end of the chromosome and less for regions toward the right. Figure 30 is a similar graph with dotted lines connecting regions ending at forked, garnet, vermilion and cut. The lines on this graph again form a fairly regular series.

The regularity of the lines on both graphs indicates that interference is lowest in the rightmost (*g–f*) region covered by the data, increasing gradually to the leftmost (*sc–cv*) region. Since the data do not include the region of 10 or 12 units from forked to the spindle-fiber attachment, the amount of interference in that region is uncertain. But interference is apparently very low in the neighborhood of the spindle fiber in the second and third chromosomes. It is probable that, for the X-chromosome, interference is lowest in the neighborhood of the spindle fiber, increasing gradually and consistently from right to left, i.e. from the spindle-fiber attachment to the free or distal end.

SUMMARY

The data of Bridges and Olbrycht (1926) and Anderson (1925) on crossing-over in the X-chromosome of *Drosophila melanogaster* are examined with reference to the distribution of interference.

Interference may be measured by the formula

$$\frac{y - 0.5\,(1 - e^{-2x})}{x - 0.5\,(1 - e^{-2x})},$$

where x is the amount of crossing-over, y is the amount of recombination, and e is the base of natural logarithms. This measure is applicable in cases where the percentages both of crossing-over and of recombination can be determined.

Numerical values of the quantity $0.5\,(1 - e^{-2x})$ are tabled for values of x from 0.11 to 1.00.

By an application of this method of measurement, interference is shown to be lowest at the right or spindle-fiber end of the X-chromosome, increasing gradually toward the left or distal end

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THE EFFECT OF CYANIDES ON THE PLASMA MEMBRANE

FLOYD J. BRINLEY

PHYSIOLOGISTS and morphologists have been interested in the function and structure of the cell since its discovery in 1665 by Robert Hooke (Locy), who, as is well known, did not observe the living cell, but only the dead cellulose wall. The early investigators in the seventeenth century confined their study to the cellular structure of tissues and paid very little attention to the nature of the cell. After the rediscovery of protoplasm by von Mohl in 1846, the interest of scientists was quickly turned to a study of the living contents of the cell. (Protoplasm had previously been noticed *in animal cells and called* "sarcode" by Dujardin.) From the time of von Mohl until the present, biologists have been interested in the study of the physical and, to a lesser extent, the chemical nature of the living substance of the cell. There is much evidence to show that the protoplasm is not of the same structure throughout the cell, for the internal protoplasm is physically and perhaps chemically different from the outer layer, which behaves as a semipermeable membrane (plasma membrane). At the present time it is generally recognized that the plasma membrane plays a very important rôle in the life of the cell, for all food materials used and the waste material produced by the internal protoplasm must pass through the plasma membrane. Therefore the permeability of the plasma membrane has become a subject of study by biologists and many papers on it have appeared in scientific literature.

It has long been known that weak acids and alkalies penetrate the plasma membrane with little if any resistance, while the living membrane is practically impermeable to strong acids and alkalies. Osterhout and Dorcas (1925) were among the first investigators to make a careful quantitative study of the permeability of the plasma membrane to weak acids These investigators immersed cells of the marine alga (Valonia) in sea water containing CO_2 or H_2S After equilibrium had been established between the cell and its environment, the contents (sap) of the cell were analyzed for total sulfide and carbonate It was found by these workers that the amount of acid which had penetrated the plasma membrane was in direct proportion to the molecular concentration of CO_2 and H_2S in the external solution From these results Osterhout and Dorcas concluded that most of the CO_2 and H_2S entered the cell in the form of undissociated molecules and not as ions, thus proving conclusively the statements of other workers (Harvey, 1911, Jacobs, 1920, Beerman, 1924, Bodine, 1924) that weak acids, carbon dioxide, hydrogen sulfide and hydrogen cyanide enter cells or pass through living membranes (protozoa or frog skin) in the form of undissociated molecules and that the membranes, as long as they remain uninjured, are impermeable to the ions It was assumed, therefore, by these latter investigators that the greater toxicity of the weak acid as compared with the strong acids is due to the ease of penetration of the weak acids and to intracellular ionization

FURTHER STUDIES ON THE PENETRATION OF HYDROGEN CYANIDE

In 1925 the present writer (Brinley, 1927) undertook a detailed study of the effect of various factors on the penetration of HCN through living membranes Artificial cells were contsructed by stretching frog skin over one end of a hard glass tube 7 cm long and 1 5 cm in diameter A cell tube (with frog skin over one end) was then placed in a wide-mouthed bottle and the bottle and "cell" were fitted with rubber stoppers The "cell" was filled with a borax boric acid buffer solution and the bottle surrounding it was filled with the borax buffer containing HCN The pH of the internal and external solutions was varied by changing the proportion of borax to boric acid After equilibrium had been reached between the cell and its environment, the internal and external concentration of cyanide was determined by analysis and it was found that the concentration of intracellular cyanide was in direct proportion to the concentration of undissociated molecules in the external solution The penetration curve closely approximates the dissociation curve Therefore it seems evident that hydrogen cyanide penetrates frog skin mostly in the form of undissociated molecules and not as ions Studies of the effect of cyanide on the potential difference of the frog skin indicate that the molecules of HCN are actually more toxic than the ions to the skin when immersed in the HCN solutions Experiments on living organisms, Daphnia and tadpoles, gave relatively the same results as the experiments on the artificial cells, i e the animals die more quickly in the solutions in which the HCN penetrated the frog skin most readily Also studies on Elodea cells, immersed in HCN solutions with different pH values, showed that the streaming of the protoplasm ceased sooner in the acid solutions than in the alkaline Similar results from more recent experiments by Bodine (1928), on Fundulus embryos, indicate that the toxicity of HCN is directly proportional to the number of molecules of cyanide in the solution These experiments on artificial cells and living organisms show conclusively that solutions of HCN containing the largest number of molecules are more toxic than solutions of the same total cyanide concentration, but with the molecules dissociated It is evident, therefore, that the toxicity of HCN is in some way associated with the number of molecules in the solution

THE EFFECT OF INJECTIONS OF CYANIDE INTO THE CELL

The methods used by the majority of previous workers in studying the effect of acids and alkalies have been confined for the most part to immersion of the organisms in the solutions and then studying their behavior This method gives but little reliable information concerning the specific effect of the reagent on the cell The immersed cell may be affected in a number of ways the reagent may act on the plasma membrane, it may affect the internal protoplasm without injuring the membrane, or it may affect both the membrane and the internal protoplasm Until the advent of the micropipette (Barber, 1911, Kite, 1915, Chambers, 1922) it was not always possible to ascertain in what way the substance affected the cut or reacted with it Barber (1911), Chambers (1926), Reznikoff (1928) and others have brought to light by micro-injection studies many facts concerning the differences between the plasma membrane and internal protoplasm and the differences in their reactions to various chemicals Reznikoff and Chambers immersed amoebae in solutions of CO_2 and various carbonates and also injected these solutions into the cell They concluded from their results that the intracellular CO_2 concentration is not an important factor in the production of lethal effects and that amoebae are irreversibly injured only when CO_2 destroys the plasma membrane

It was reported in a previous paper (Brinley, 1928) that, when amoebae are immersed in solutions of HCN varying in concentrations from N/10 to N/3000, the plasma membrane dissolves and the cell disintegrates The time of death varies from a few seconds to forty-eight hours, depending upon the concentration of cyanide Amoebae injected with the same solutions of cyanide recover in a short time unless the dosage is so large that it ruptures the membrane Similar results (Brinley, 1929) were obtained with hydrogen sulfide, i e the organisms recover when injected with aqueous solutions of H_2S, but when immersed in this sulfide solution the cell disintegrates In a later paper the present author (Brinley, 1930) cited experiments which indicate that injections of KCN into fertilized Arbacia eggs do not delay cleavage although cell division is delayed when the eggs are immersed temporarily in the cyanide solution It has also been reported (Brinley, 1929) that ammonium hydroxide and certain ammonium salts affect the cell by virtue of their action on the plasma membrane

DISCUSSION

It seems evident from the results of the micro-injection experiments that solutions of carbon dioxide, hydrogen cyanide, hydrogen sulfide and ammonium hydroxide are not lethal when injected into cells (amoeba and Arbacia eggs), the cells, however, are killed or seriously injured when immersed in these same solutions There seem to be several possible explanations of the foregoing facts (1) the chemicals may affect the plasma membrane and not the internal protoplasm, (2) the introcellular reagents may be rapidly oxidized or united with some constituent of the protoplasm producing a non-toxic compound, or (3) the chemical rapidly diffuses out of the cell The first of these hypotheses has been discussed elsewhere (Brinley, 1930) and so it will be sufficient to say here that other investigators have found that cyanide (KCN or HCN) does have some effect on the plasma membrane, especially on its permeability Lillie (1918) states that the increase in permeability of Arbacia eggs after fertilization is reversibly retarded by KCN solutions in concentration of N/100 to n/400 Blumenthal (1927) suggested that KCN produces a decrease in permeability of the cell membrane of Arbacia eggs to water, but that HCN increases it An additional reason for believing that the action of cyanide is a surface one is the fact that some internal development, such as mitotic figures in Arbacia eggs, continues when the eggs are immersed in the cyanide solution This continuation of internal development of Arbacia eggs when placed in cyanide was studied by Heilbrunn (1920), who contends that in the normal developing egg there is an increase in the viscosity of the protoplasm to a certain stage, where the process becomes reversible and the viscosity is decreased In the presence of cyanide, Heilbrunn states, the gelation of the protoplasm is intensified and the normal decrease in viscosity which occurs during the mitotic process is rendered reversible and further development cannot take place Thus development proceeds as far as the formation of the spindle and then stops However, it may be possible to explain this reaction in some other terms, such as a change in the colloidal nature of the plasma membrane, which may accompany the internal protoplasmic changes If the effect of cyanide is due to some action on the cell membrane, may it not be assumed that internal development would continue to a certain stage where for further development the process depends upon some change in the membrane which is prevented from occurring by the cyanide?

The second possible explanation of the fact that injections of cyanide do not irreversibly injure cells is that the intracellular cyanide may be oxidized by the protoplasm or bound by some constituent of the cell It has been shown by Baker and DeLong

(1927) that glucose will oxidize hydrogen cyanide, liberating ammonia Shafer's papers (1911 and 1916) and unpublished work by the author seem to indicate that cyanide is not recoverable from certain insects (*Passulus cornutus*) after they have been anaesthetized with hydrogen cyanide These experiments indicate that the cyanide has been changed in some manner It is entirely possible that intracellular oxidations may play an important rôle in the recovery of a cell from sublethal concentrations of cyanide, but this factor alone probably does not account for the recovery of cells which had been injected with large dosages of concentrated cyanide solutions Amoebae will recover from large dosages of N 10 KCN or HCN solutions, but if the cells are immersed in N 300 cyanide solution they die within a few minutes The intracellular concentrations of cyanide resulting from injections of N/10 HCN solution is undoubtedly greater than would result from immersion of the cells in more dilute solutions Hence, if the internal oxidation of the cyanide is the controlling factor in the recovery of the cell from injections of cyanide, it would follow that injected cells containing a high intracellular concentration of cyanide would be irreversibly injured However, as has previously been stated, cells recover from injections of large dosages of concentrated cyanide solution

It may also be assumed that the non-lethal effect of injected cyanide is due to its rapid diffusion out of the cell, this, however, may be ruled out by the fact that amoebae immersed in hydrogen cyanide solution and immediately injected with the same acid do not die any sooner than uninjected cells immersed in the same solution A number of amoebae were immersed in N/300 HCN solution and immediately injected with N/100 HCN solution By this means a much higher initial intracellular cyanide concentration was obtained than would result from immersion without injection Unless the cyanide was changed or bound in some way, it would probably diffuse out of the cell until equilibrium was reached between the cell and external solution, but the rate of diffusion would be slower than if there were no cyanide in the external solution If the non-lethal action of injected cyanide is due to its rapid rate of diffusion out of the cell, the organisms should die in a shorter time when the rate of diffusion is reduced This, however, as we have seen, does not occur

From the data presented it appears that the toxicity of hydrogen cyanide, hydrogen sulfide and ammonia to amoebae and Arbacia eggs is the result of some effect on the plasma membrane and not on the internal protoplasm

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NOTES AND STUDIES ON ARACHNIDA I

ARANEAE FROM THE LANCETILLA VALLEY, HONDURAS I

ARTHUR M CHICKERING

As A collector for Albion College and the Botanical Gardens of the University of Michigan I spent six weeks in June and July, 1929, at the Lancetilla Experiment Station located about six kilometers south of Tela, Honduras This Station is operated by the United Fruit Company for the study and introduction of new horticultural and agricultural products into Central America, and for the study of problems arising from the banana-raising interests of that region In addition to general collecting of plants and animals I was able to procure a fairly representative collection of Arachnida, a group of animals to which I am devoting some study at the present time

Lancetilla Station is located in the very beautiful Lancetilla Valley at an altitude of about 60 feet Its site is an abandoned banana farm Except where the land is being cultivated, the valley floor is covered with a dense growth of small trees, shrubs, vines and tall grasses in places almost impenetrable The surrounding hills rise very abruptly to a height of about 2000 feet They are covered with virgin forest and offer attractive collecting grounds to every naturalist The region has been elevated recently and is being dissected by many swift mountain streams which add much to the natural beauty of the valley Near the mouth of the Lancetilla River and at several other neighboring places are lagoons and marshes where many interesting animals and plants can be found As noted by Standley, the strand vegetation near Tela has more than passing interest for both zoologists and botanists

This whole region seems to be well suited to work of many kinds

Large animals are common and frequently encountered in the forests Poisonous snakes are present, but do not seem to be common It is well, however, to carry antivenin for use quickly in case of need This can be procured in Tela The venom used in the production of antivenin is obtained from snakes kept at the serpentarium located near the Station and maintained by Harvard University, Tela Railroad Company and H K Mulford Company

Work on the flora of the Lancetilla Valley has been carried on by Standley (3), who has made a comprehensive survey of the region Peters (2) and Bangs have collected birds in the vicinity Insects and fishes have received some attention I hope to add to the knowlege of the Arachnida through study of my collections Dr Wilson Popenoe, director of the Station, takes a friendly interest in all kinds of biological work in the valley and uses every opportunity to encourage investigation I am glad to take this opportunity to thank Dr Popenoe and his staff for the many courtesies extended to me during my stay at Lancetilla Without their interest and cooperation my work would have been impossible

My collections were made from as many different localities as possible It is probable that I have two hundred species of spiders as well as a number of other arachnids The study of these is going forward, but progress is slow on account of the difficulty of procuring the necessary literature The present paper constitutes a modest beginning of what I hope will be a series of papers dealing with the taxonomy, life-histories and general biology of this group of animals Unless otherwise stated all species listed below are from the Lancetilla Valley

ARGIOPIDAE

METINAE

HENTZIA TRIVITATTA (Cambridge) — Not common, but two specimens taken, both females

LEUCAUGE ARGYRA (Walkenaer) — Common throughout the valley Just back of the strand region in the vicinity of Tela, among the thick vegetation, this spider is abundant. It often builds its webs high in the trees here, and they are often more or less connected with one another.

Leucauge aurostriata (Cambridge).—One female. Formerly reported only from Mexico.

Leucauge idonea (Cambridge).—Common, but not abundant, as in the case of *L. argyra*.

Leucauge moerens (Cambridge).—Appears to be fairly common.

NEPHILINAE

Nephila clavipes (L.).—Quite common. Found chiefly around buildings. Mature in July. Much less common than at Barro Colorado, where it is one of the most conspicuous forest spiders.

GASTERACANTHINAE

Gasteracantha kochi Butler.—Very common in sheds and other buildings.

Micrathena bimucronata (Cambridge).—Not common, but one specimen taken, a female. Also reported from Guatemala.

Micrathena brevipes (Cambridge).—Three specimens. Probably not common.

Micrathena gracilis (Walkenaer).—This is one of the most striking of the Micrathenae seen at Lancetilla. As an adult it has a fine old-gold color, is large and robust.

Micrathena longicauda (Cambridge).—Banks (1) states that this must be the male of *M. mammillata*. It may be so. I have not taken a male *M. mammillata* from the web of a female. One specimen only.

Micrathena mammillata (Butler).—This curious spider seems to be common here, but is much smaller than in Panama.

Micrathena obtusispina (Keyserling).—This is the most common of the larger Micrathenae, and seems to agree well with typical forms figured by Cambridge.

Micrathena patruelis (C. Koch).—This is the most common of all the Micrathenae. Obtained almost everywhere.

Micrathena sagittata (Walkenaer) — Taken only at Progreso, not in the Lancetilla Valley One female

Micrathena sp ? — One female, taken at 1200 feet altitude in the forest May be a new species Eight abdominal spines, red tipped with black Abdomen white dorsally Total length about eight millimeters

Micrathena sp ? — Two females May also be a new species Eight abdominal spines Abdomen black dorsally with yellow and white spots, black ventrally with deep yellow spots Total length about seven millimeters

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SPERMATOGENESIS OF *RANATRA FUSCA* (P. B.) HUNGF.

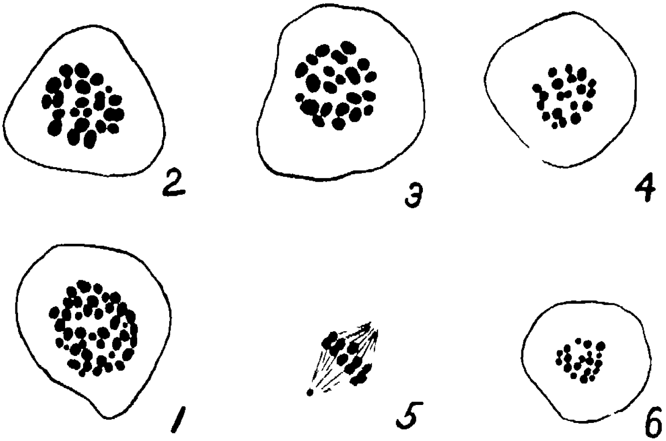
ARTHUR M. CHICKERING, HOWARD M. FIELD AND
HOMER A. HOWES

PREVIOUS work on spermatogenesis in Ranatra has been published by Chickering (1918) and Steopoe (1927). Chickering reported two types of testes in material not clearly separated into two species. The first type was regarded as having spermatogonia with forty chromosomes of various sizes, primary spermatocytes with twenty-one, secondary spermatocytes with twenty-one, two of which behaved as an XY-pair. Thus each spermatid was believed to receive nineteen autosomes and either an X- or a Y-chromosome. Meager observations on the second type seemed to indicate the presence of eight or ten additional chromosomes in the spermatogonia. A characteristic group of small chromosomes was observed near the center of the equatorial plate in primary and secondary spermatocytes. In *R. linearis*, collected near Bucharest, Roumania, Steopoe has reported spermatogonia with forty-three chromosomes, all of similar size and form except five which behave as sex-chromosomes during the maturation period. The primary spermatocytes were found to possess twenty-four chromosomes each (nineteen bivalents plus five univalents), and the secondary spermatocytes had a like number. The second division occurred in such a manner that two kinds of spermatids were produced. One kind of spermatid thus appeared to receive nineteen autosomes plus the largest of the group of five sex-chromosomes, and the other kind received nineteen autosomes plus the remaining four small sex-chromosomes.

The differences noted between the spermatogenesis of the European *R. linearis* and the American species suggested a reëxamination of the material studied by Chickering. It was impossible to study the original material which had been collected in the vicinity of Beloit and Madison, Wisconsin, because this, in the meantime, had been destroyed by fire Specimens collected at Albion and Ann Arbor, Michigan, in the summer of 1924, however, had yielded well-fixed and stained material Additional material was collected and prepared in the usual ways by the junior authors during the latter part of September and the early part of October, 1929 Testes from these specimens were shrunken and relatively inactive, and yielded few stages suitable for counting chromosomes Animals kept in the laboratory and killed later in the winter yielded testes which were still smaller and less active, while the seminal vesicles were markedly distended The material collected and prepared by the senior author in the summer of 1924 was found to be most favorable for study, and hence it has formed the basis for the conclusions given in this paper The species collected during the past fall has been definitely identified by J R de la Torre-Bueno as *R fusca* (Palisot de Beauvois) Hungf (= *R. americana* Mont), but we think the species collected in 1924 is also *R fusca*

The spermatogonia in *R fusca* are believed to contain forty-two chromosomes of various sizes, but quite uniform in shape (Fig 1) Considerable difficulty has been encountered in determining this number, owing to the minute size of some of the chromosomes and the tendency toward crowding The primary spermatocytes possess twenty-two chromosomes, three of which tend to group themselves together in the center of the equatorial plate (Figs 2–3) These all divide at about the same time The secondary spermatocytes show twenty-one chromosomes in each cell in polar view (Fig 4) Lateral views of these cells in metaphase show a pair of chromosomes arranged end to end (Fig 5) This pair is believed to represent an XY-pair of sex-chromosomes, and their position explains the fact that in polar views one chromosome less than the expected number is seen These two chromosomes separate precociously, and are frequently advanced toward the poles of the spindle before the autosomes divide Although it has been difficult to find clear spermatid groups of chromosomes, it is believed that each spermatid receives twenty-one (Fig 6)

PLATE XXXVIII



Ranatra fusca (americana)

Fig 1 Polar view of metaphase of a spermatogonium showing forty two chromosomes

Figs 2 3 Primary spermatocytes in metaphase showing twenty two chromosomes in each

Figs 4 5 Metaphases of secondary spermatocytes Twenty-one chromosomes are visible in Figure 1

Fig 5 The XY pair in the center separating in advance of the division of the autosomes

Fig 6 The spermatid complement of chromosomes twenty one of which are here shown

The results can be explained most readily by considering that there is an XY-pair of chromosomes present and that the primary spermatocytes contain twenty bivalents and two univalents The first maturation division is probably reductional for autosomes and equational for the XY-pair The second division is probably equational for autosomes and reductional for the sex-chromosomes, thus resulting in passing twenty-one chromosomes into each spermatid (twenty autosomes and either an X- or a Y-chromosome)

Another species taken with *R fusca,* but not yet definitely identified, is probably the same as the second type mentioned by Chickering (1918) in his earlier note We have observed that the primary spermatocytes have almost the same appearance as those described for *R linearis* by Steopoe, with the exception that we find one small additional chromosome lying off at one side of the main group There is also a very characteristic group of five chromosomes located near the center of the equatorial plate This leads us to the belief that this species and the second one mentioned in 1918 are identical and that they are alike in possessing a chromosome complex very similar to that of *R linearis* as described by Steopoe

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THE MICHIGAN DECAPOD CRUSTACEANS

EDWIN P CREASER

IN 1910 Dr A S Pearse published an account of the Michigan crayfishes, describing and figuring the species then known or reported from the state Since that time an abundance of crustacean material has been collected by the State Department of Conservation and by the Fish and Crustacean Divisions of the Museum of Zoölogy This rich material makes possible now a more detailed treatment of the distribution of the decapods in Michigan

Two families of decapod crustaceans are represented in the Michigan fauna All the crayfishes are representatives of the family Astacidae Eight species of the genus *Cambarus* are now known to occur within the state The family Palaemonidae, essentially a marine group, is represented by the shrimp, *Palaemonetes exilipes* Stimpson All these are described and figured in the present paper

FAMILY ASTACIDAE

Identification of the species of *Cambarus* is based largely upon the structure of the modified first abdominal appendage of the male, which is used as a copulatory organ This organ undergoes a seasonal change so that two forms of the sexual appendage occur The differences between the two forms are sometimes very striking First form males can usually be distinguished by the horny color of the outer of the two rami of the appendage Identification of female specimens is possible from the structure of the carapace, chelae and annulus ventralis The terminology used in the key which follows is explained in a glossary and figure at the end of this paper

KEY TO THE MICHIGAN CRAYFISHES

1 a Sexual organ of male terminating in two slender elongated tapering tips *either straight or gently curved* *Third walking legs with hooks* on third segment Michigan species of subgenus *Faxonius*

2 a Both tips of male sexual organs curved posteriorly

3 a Rostrum with subparallel sides moderate lateral spines and short acumen Antennal scale uniformly rounded Chelae moderately broad, movable finger with straight cutting edge Length of posterior section of carapace contained less than twice in the length of the anterior section Male sexual organs gently curved Female annulus ventralis with a median transverse fossa
C (*Faxonius*) *virilis* Hagen (Fig 31)

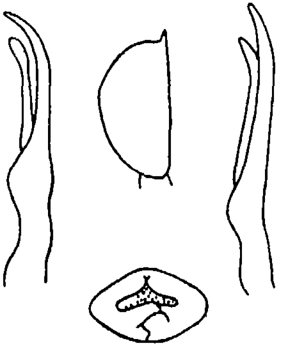


FIG 31 First and second form male sexual organ antennal scales and annulus ventralis of *C virilis*

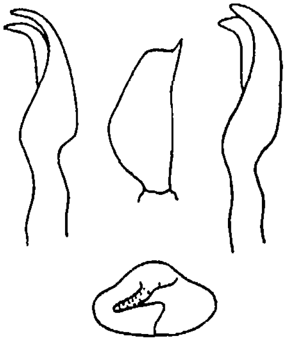


FIG 32 First and second form male sexual organ antennal scales and annulus ventralis of *C immunis*

3 b Rostrum convergent, with short acumen and with or without lateral spines Antennal scale irregularly rounded Chelae narrow, movable finger with incision at base on inner side Length of posterior section of carapace contained twice in the length of the anterior section Male sexual organs abruptly curved Female annulus ventralis with a deep fossa to the left as viewed from the ventral side
C (*Faxonius*) *immunis* Hagen (Fig 32)

2 b Tips of male sexual organ straight

4 a Rostrum with converging sides and a well-developed median carina or elevation above Sexual organ stout,

with short tips outer tip about the same length as the inner which is smooth at the apex Anterior margin of first form sexual organ smooth Annulus ventralis flat usually without a fossa or with an irregular one following the curve of the sinus

C (*Faxonius*) *propinquus* Girard (Fig 33)

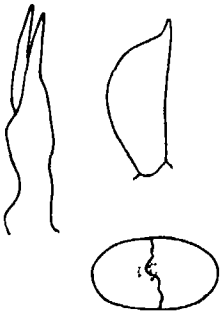


Fig 33 First and second form male sexual organ, antennal scale and annulus ventralis of C *propinquus*

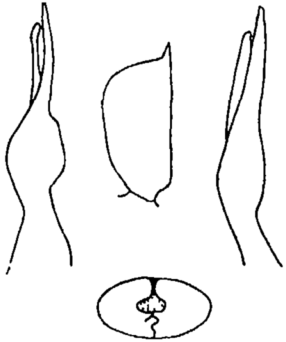


Fig 34 First and second form male sexual organ antennal scale and annulus ventralis of C *rusticus*

4 b Rostrum with slightly convex sides, smooth or faintly carinate above Sexual organ slender, with long tips, outer tip exceeding the inner which is dilated or swollen at the apex Anterior margin of sexual organ of first form males with a shoulder or angle Annulus ventralis bituberculate anteriorly, with a short median transverse fossa

C (*Faxonius*) *rusticus* Girard (Fig 34)

1 b Sexual organ of male terminating with two short tips curved at about right angles with the main shaft the outer of the two tips (the top one) flattened laterally the inner one rounded Hooks on the third segment of the third walking legs in the male (See also item 1 c below) Michigan species of subgenus *Bartonius*

5 a Areola visible throughout its entire length Carapace wider than high

6 a Rostrum moderately long without lateral spines Chelae ribbed and coarsely punctate Areola about as wide as antennal scale Cephalothorax flattened above Length of posterior section of carapace contained twice in the distance from point of attachment of abdomen to posterior joint of the telson Sexual organ of male with both

tips curved posteriorly about the same distance Annulus ventralis with a raised posterior margin, and a fossa following the sinus, which is curved to the left as viewed from a ventral aspect *C* (*Bartonius*) *robustus* Girard (Fig 35)

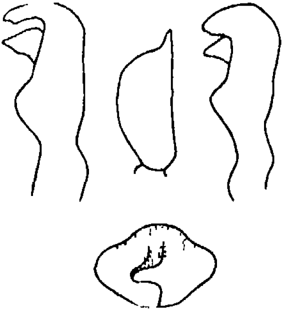


Fig 35 First and second form male sexual organ antennal scale and annulus ventralis of *C* *robustus*

5 b Areola obliterated Carapace higher than wide

7 a Movable finger of chela with a straight cutting edge Anterior margin of carapace with a triangular protuberance behind the antennal scale Length of posterior section of carapace contained less than twice in the distance from point of attachment of abdomen to the posterior joint of the telson Annulus ventralis flat, with sinus curved to the right from ventral aspect, fossa short, median and transverse *C* (*Bartonius*) *diogenes* Girard (Fig 36)

7 b Movable finger of chela with an incision at the base on the inner margin Anterior margin of carapace nearly straight behind the antennal scale Length of posterior section of carapace contained more than twice in the distance from point of attachment of abdomen to the posterior joint of the telson Annulus ventralis with raised posterior margin, sinus curved to the left from ventral view, fossa shallow, extending from the anterior margin to the curve in the sinus *C* (*Bartonius*) *fodiens* (Cottle) (Fig 37)

1 c Sexual organ of male truncate or blunt at the tip, other part ending in three rather short teeth, inner part terminating in an acute spine Hooks on third and fourth walking legs Michigan species of subgenus *Cambarus*

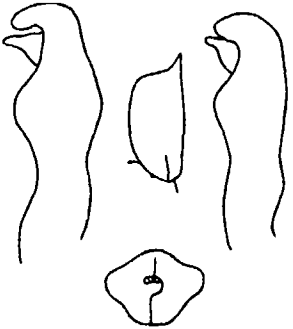


Fig 36 First and second form male sexual organ antennal scale and annulus ventralis of *C diogenes*

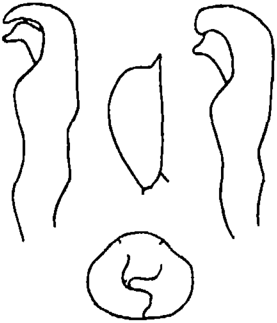


Fig 37 First and second form male sexual organ antennal scale and annulus ventralis of *C fodiens*

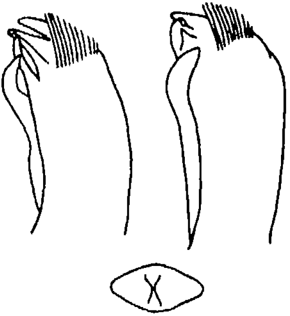


Fig. 38 First and second form male sexual organ and annulus ventralis of *C blandingii acutus*

8 a Chelae long and subcylindrical with scale-like tubercles above Antennal scale irregularly rounded Rostrum long, with short acumen and converging sides Cephalothorax granulate on the sides Areola narrow and smooth Male sexual organ with a row of setae on the outer side near the apex Annulus ventralis with a straight sinus between two tubercles

C (Cambarus) blandingii acutus Girard (Fig 38)

DISCUSSION OF NOMENCLATURE

The subgeneric names are included in this paper, since it is my belief that they will eventually receive generic ranking As early as 1870 Hagen (1870, p 29) wrote as follows "With reference to the further division of the genus *Cambarus*, it was especially important to decide whether all North American Cambari belonged to the same genus or to different genera I am now convinced that all the species I have seen form only one genus, containing several more or less well-defined groups In this manner the genera *Cambarus* and *Astacus* seem very natural and of equal value But I have no doubt that some time the genus *Astacus* will be divided into three genera (for the European, North American, and Asiatic species), and *Cambarus* into three or it may be into six genera as Prof Agassiz thinks"

Ortman (1905*a*, pp 96-97, 1905*b*, p 437) has clearly defined five groups of *Cambarus* and has given them subgeneric names A consideration of Ortman's groups as genera should await the much needed monographic treatise of all the crayfishes

The form of *Cambarus immunis* called *C immunis spinirostris* by Faxon is not considered here as a true geographical subspecies Specimens without spines on the rostrum occur in the same ponds with individuals bearing spines

The distribution of *C robustus* has been studied by Ortman in Pennsylvania, Turner in Ohio, and Newcombe in West Virginia This species of the *Bartonius* group was not found by any of these men to intergrade with the species called *C bartonii bartonii*

C bartonii bartonii has never been taken in Michigan although Williamson (1907, p 133) found it in a small creek draining into Lake Superior near Searchmont, in Algoma District, Ontario

Cambarus robustus is unique in having the posterior section of the carapace elongated as contrasted with the abdomen The chelae and rostrum as well as the sexual organs also differ from those of the other species of this group In view of these facts I regard this form as specifically distinct rather than as a subspecies of *C bartonii* It is my belief that the species described by Faxon as *C bartonii veteranus* is the same as *C robustus* Old individuals exhibit the peculiar gaping chelae, the character used by Faxon to differentiate *veteranus*

Huntsman (1915, p 158) has recently shown that *C argillicola* Faxon is a synonym of *C fodiens* (Cottle) Ortman (1905, p 123) thought that *C fodiens* might be regarded as a local form of *C diogenes* These species have distinct habitat preferences, the eggs appear at different times, and there are some very distinct morphological differences Thus there can be no doubt that they are very distinct species

Palaemonetes paludosa (Gibbes) is here considered a synonym of *Palaemonetes exilipes* Stimpson

DISTRIBUTION AND HABITS OF MICHIGAN CRAYFISHES

1 *Cambarus virilis* Hagen

Range — Chihuahua, Mexico, Texas, Oklahoma, Kansas, Missouri, Colorado, Iowa, Minnesota, Nebraska, North Dakota South Dakota, Wisconsin, Michigan, Illinois, Indiana, Ohio, Pennsylvania, New York, Ontario, Saskatchewan and Manitoba

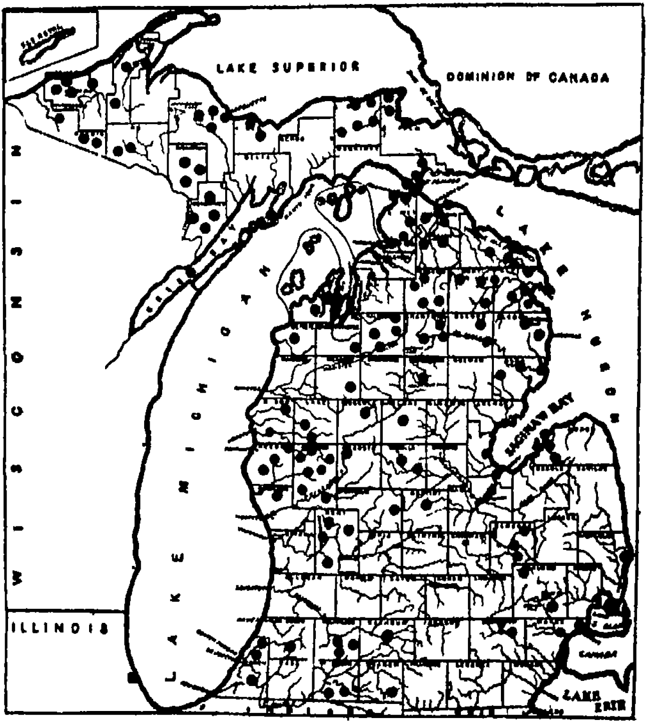
Distribution in Michigan (Map 3) — *Cambarus virilis* is found in all the major drainage areas of the state A stock of this species from Green Bay of Lake Michigan has been planted in some of the lakes of Marquette County

Ecology — This species occurs very abundantly throughout Michigan in streams, rivers and lakes, and has a decided habitat preference for a stream bottom with stones, under which it may hide *Cambarus virilis* occurs in midsummer in even the coldest streams, where the fish fauna is limited to *Cottus*, the miller's-thumb, and *Salvelinus*, the brook trout The eggs are found attached to the female usually before the last of April These crayfishes are of a dusky brown hue

2 *Cambarus immunis* Hagen

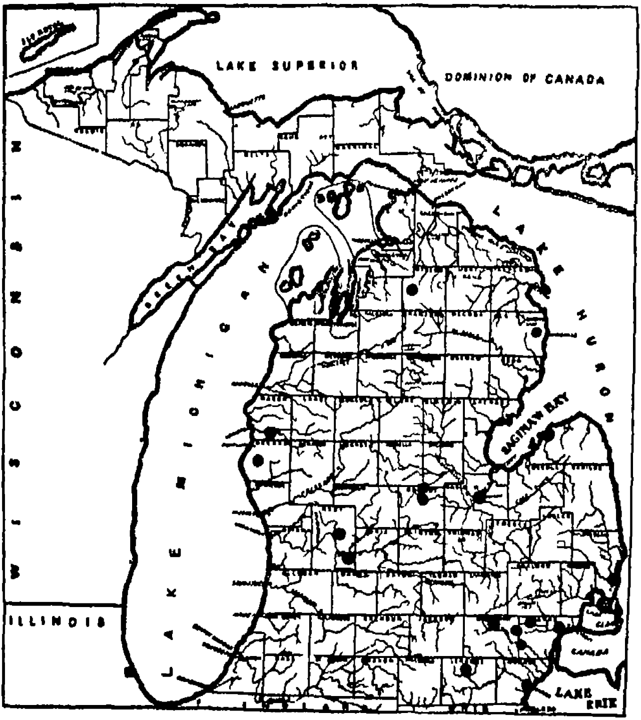
Range — Colorado, Oklahoma, Kansas, Missouri, Nebraska, Iowa, Wyoming, North Dakota, Minnesota, Wisconsin, Illinois, Indiana, Ohio, Michigan, southern Ontario, New York and Massachusetts

Distribution in Michigan (Map 4) — *Cambarus immunis* is found at the present time northward as far as Otsego County in the Lower Peninsula The possibility that it may occur farther north illustrates the need for collections from the shallow-pond fauna of the regions north of the Straits of Mackinac



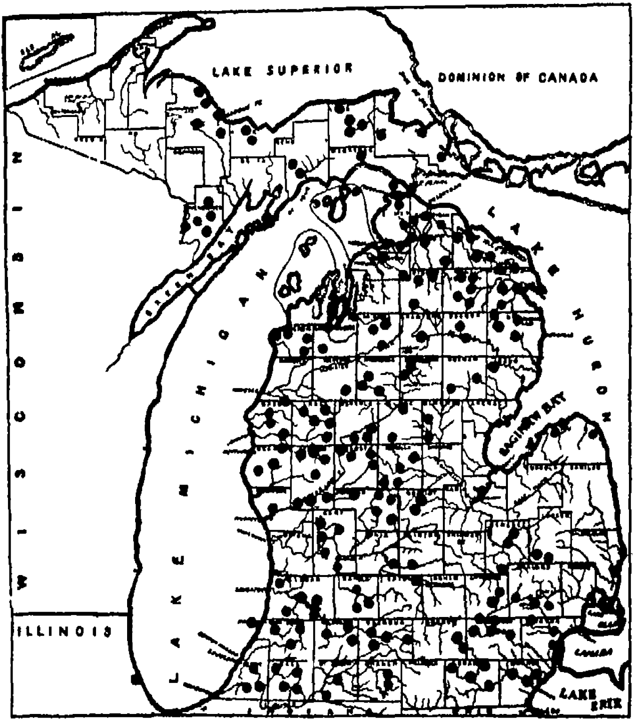
Map 3 Distribution of *C virilis* in Michigan

Ecology — *Cambarus immunis* occurs in greatest abundance in stagnant ponds It is sometimes found in slowly moving waters or in lakes, and has a decided habitat preference for muddy bottoms, in which it may partially bury itself In temporary ponds *Cambarus immunis* resorts to shallow burrows during the dry season



MAP 4 Distribution of *C immunis* in Michigan

son Females with eggs attached are found late in November when the ice is just forming on the pond and in the latter part of February when the ice is just breaking up The carapace and abdomen are olive-green mixed with brown, the color varying



MAP 5 Distribution of *C propinquus* in Michigan

somewhat with the environment On the dorsal side of the abdomen and carapace a lighter color forms a contrasting design The chelae are tipped with red A blue color phase has been found in Michigan

3 *Cambarus propinquus* Girard

Range — Quebec, Ontario, Michigan, Wisconsin, Iowa, New York, Pennsylvania, Ohio, Indiana and Illinois The record for Chihuahua, Mexico, although well attested, needs to be confirmed

Distribution in Michigan (Map 5) — *Cambarus propinquus* is found in all the major river systems in the state and is our commonest species

Ecology This species, which is found in rivers, lakes and streams, has a habitat preference similar to that of *Cambarus virilis* Females with young attached were taken near Marquette and Ann Arbor in June This species is an important item in the food of the rainbow trout In the stomach examinations made of this fish taken from various localities in Michigan, fifty seven specimens of this crayfish were found The only other species found was *Cambarus diogenes*, of which there were three specimens *Cambarus propinquus* is brown, with orange-tipped chelae A blue color phase has been found in Michigan

4 *Cambarus rusticus* Girard

Range — Kentucky, Ohio, Michigan, Indiana, Illinois, Tennessee, Iowa and Missouri There is reason to doubt the records from states other than these

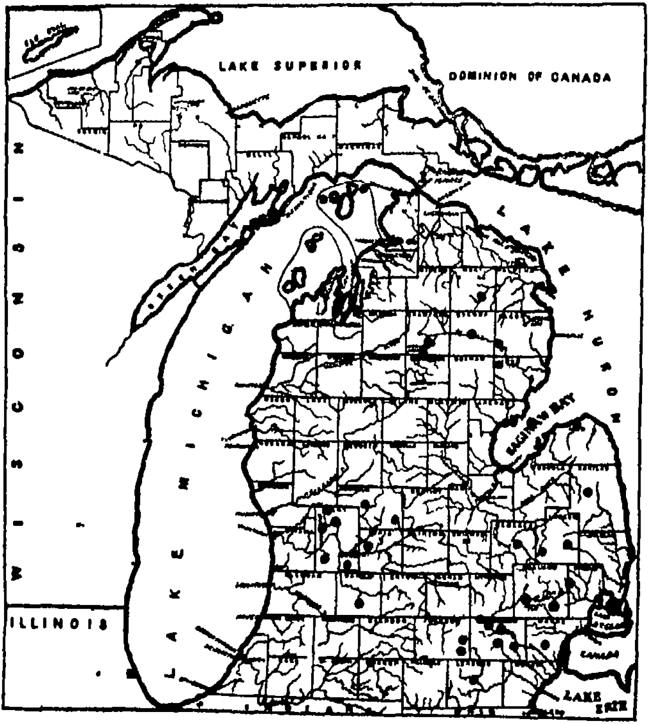
Distribution in Michigan — The records for Michigan given previously by Faxon (1884, p 148, 1898, p 658) are doubtless erroneous The new records from streams of the Maumee River drainage area in Lenawee County fit in well with the general range of the species, which, in brief, is the Ohio River and its tributaries The Maumee River and the Ohio River have been connected by a canal During flood periods some of the streams of the two rivers are confluent, allowing by this means also an exchange of fauna

Ecology — This species has been found in Michigan only in a small stream with gravel and stone bottom Many of the individuals were hiding under the stones, in company with *Cambarus propinquus* The carapace and abdomen are a greenish-brown The claws of all the walking legs are tipped with orange

5 *Cambarus robustus* Girard

Range — West Virginia, New York, Pennsylvania, southern Ontario, Michigan and Ohio

Distribution in Michigan (Map 6) — *Cambarus robustus* occurs in seven river systems draining into Lake Erie and Lake Huron It has also become established in the Grand River system which drains into Lake Michigan It will be noted from the map that this species is found in greatest abundance at the headwaters of the various river systems This is in accord with its habitat preference Its occurrence in Saginaw Bay is remarkable and an



Map 6 Distribution of *C robustus* in Michigan

explanation must await a study in that locality The failure of *Cambarus robustus* to become more widely established in the Lake Michigan drainage area may be due to environmental barriers

Ecology — *Cambarus robustus* is found most abundantly in swift shallow streams, especially those with stony bottoms It frequently lurks under the larger stones Huntsman (1917, p 132) has found that it often burrows *Cambarus robustus* is uniformly deep brown on the carapace, chelae and abdomen

6 *Cambarus diogenes* Girard

Range — Wyoming, Minnesota, Wisconsin, Michigan, lower Ontario, Pennsylvania, New York, New Jersey, Virginia, West Virginia, North Carolina, Maryland, Ohio, Indiana, Illinois, Iowa, Kansas, Missouri, Arkansas and Colorado

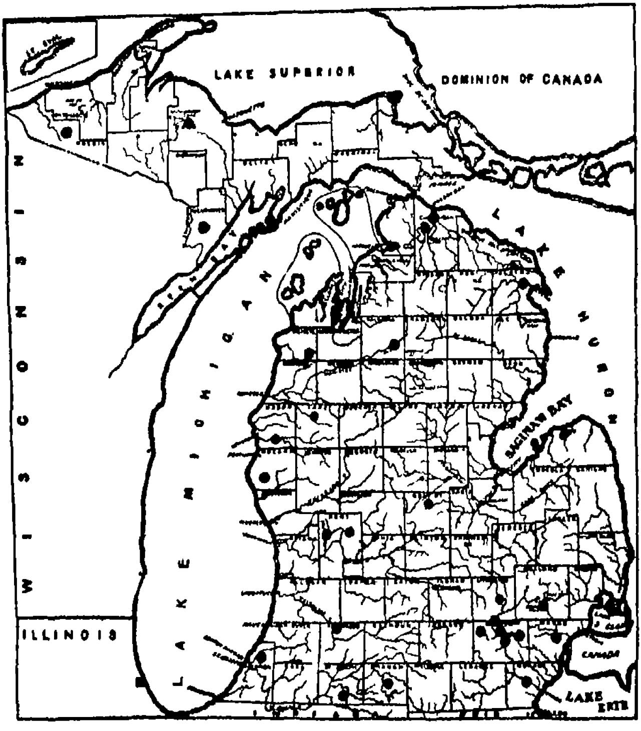
Distribution in Michigan (Map 7) — As this species is one of the burrowing crayfishes, and as most of the collections have been made in streams, its distribution is not known as well as that of some of the others It is found, however, throughout the Upper and Lower peninsulas

Ecology — This aggressive burrowing species is found in streams, rivers and lakes during the breeding season in early spring Later it returns to the burrows, which are sometimes at a considerable distance from the nearest stream or lake Moulting undoubtedly occurs soon after the breeding season, since the shed chelae and carapaces are found in great abundance during the latter part of spring Females with young are recorded by Pearse (1910, p 20) as occurring in June

7 *Cambarus fodiens* (Cottle)

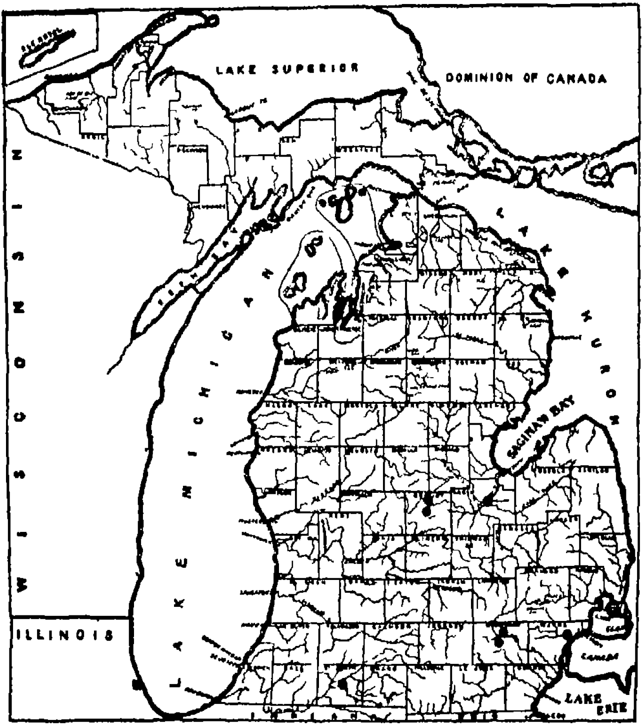
Range — Michigan, lower Ontario, Ohio, Indiana, Illinois, Mississippi and Louisiana Owing to the possibility of confusion with *Cambarus uhleri*, other records for this species should be confirmed

Distribution in Michigan (Map 8) — Because of the burrowing habits of this animal, its distribution in Michigan is also still inadequately known The record by Pearse (1911, p 130) from Cheboygan County was based on a young specimen, which on reexamination proves referable to *diogenes*



MAP 7 Distribution of *C diogenes* in Michigan

Ecology — This species is peculiar in its habitat preference for temporary woodland ponds It is found in them immediately after the snow melts in the springtime Females carrying eggs are obtained in Michigan from March to April As the season advances, these crayfishes resort to burrows, which are sometimes five feet deep This aggressive crayfish is brown, with a design outlined in black on the abdomen and cephalothorax



Map 8 Distribution of *C fodiens* in Michigan

8 *Cambarus blandingii acutus* Girard

Range — Michigan, Ohio, Indiana, Illinois, Wisconsin, Iowa, Missouri, Kansas, Oklahoma, Texas, Mississippi and Louisiana The records from the Atlantic coastal states need to be confirmed

Distribution in Michigan — The single specimen found dead by Pearse at White Pigeon in Saint Joseph County is, as yet, the only one recorded from this state[1]

Ecology — Harris (1903, p 80) cites what is known of the habits and environment of this species It apparently resorts to shallow burrows, as conditions demand, and is sometimes found in streams and rivers, where it avoids strong currents It appears, therefore, to have a habitat preference and habits similar to those of *Cambarus immunis* The carapace, chelae and abdomen are decidedly reddish, with the granular parts contrasted in green

FAMILY PALAEMONIDAE

Shrimp-like decapod crustaceans, with strongly compressed abdomen First segment of abdomen little if any smaller than the others Abdomen with a sharp bend, and with five pairs of well-developed pleopods, which are used for swimming First two pairs of legs chelate Second pair of chelae larger than the first Pleura of first abdominal segment overlapped by those of the second segment Rostrum long, immovable, compressed, armed with teeth Mandibles deeply cleft

9 *Palaemonetes exilipes* Stimpson

(Figure 39)

Mandibles without a palp or endopodite Second pair of chelae only slightly larger than first Fifth walking leg exceeding the rostrum Antennae longer than body Outer flagellum of antennule longer than inner Antennal scale rounded distally, sides subparallel, length exceeding rostrum Rostrum compressed, usually seven teeth above and two below (number variable) Second tooth of dorsal margin usually directly above the base of the eye stalk Carapace with lateral spine on anterior margin and another behind the eye Abdomen slender, curved at the end of the third segment Telson gradually tapering, ending with a median tooth and two spines Sides of telson curved inward at distal end First abdominal appendage not modified

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[1] After this paper had gone to press I obtained a living specimen from Dowagiac Creek at Niles, Berrien County, Michigan

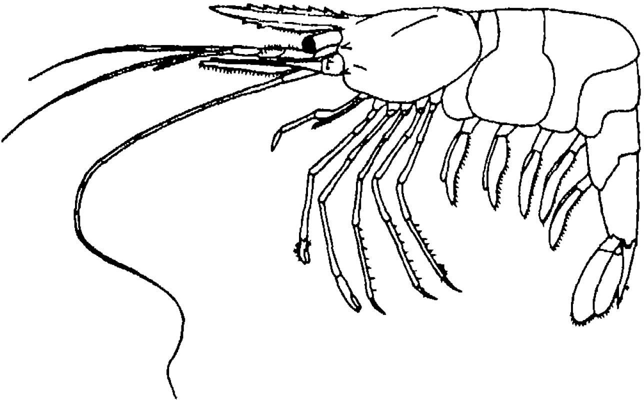

FIG 39 *Palaemonetes exilipes* Stimpson

into copulating organ Integument transparent in living animals Small crustaceans, never more than two or three inches long

Range —Iowa, Wisconsin, Michigan, Ontario, New York, Pennsylvania, Ohio, Indiana, Illinois, Kentucky, Tennessee, Arkansas, Oklahoma, Texas, Louisiana, Mississippi, Alabama, Florida, Georgia, South Carolina, North Carolina, Virginia, District of Columbia and Maryland

Distribution in Michigan — *Palaemonetes exilipes* has been previously recorded by Smith (1874, pp 641-642) from Ecorse, in Wayne County In August, 1929, Professor Hankinson and the writer obtained many of these shrimps in Swan Creek at Oldport and Newport, in Monroe County They probably occur in other Michigan streams and rivers draining into Lake Erie

Ecology — This interesting crustacean prefers slowly moving rivers and streams, or lakes and ponds which have an abundance of vegetation *Palaemonetes exilipes* attains its maximum numbers in overflow ponds of rivers, where the fish population is sparse In such a pond near the Ohoopee River in Emanuel County, Georgia, I took over a thousand specimens in a single seine haul This species is doubtless an important fish food

These animals are nearly transparent in life, but have chromatophores over the entire body. The chromatophores are particularly numerous upon the basal segment of the antennae. The gills, heart, blood vessels, muscles and intestinal tract are readily discernible in the live specimens. *Palaemonetes exilipes* is thus admirably adapted to experimental studies. It may be kept for a considerable time in an aquarium. An abundance of vegetation should be present, and an air supply is absolutely essential. I was able to keep my specimens alive for over five months.

These shrimps move either by sudden jerks or by swimming continuously forward. They are also capable of moving sidewise. Although the clawed feet are used occasionally for holding on to the leaves, they are usually doubled back beneath the body as the animal crawls from place to place of the aquatic vegetation. They are also used to scrape the food from the surface of leaves.

Shelford (1913, p. 129) found *Palaemonetes exilipes* carrying eggs early in the springtime. I have specimens of females carrying eggs which were obtained in April, July and August. This suggests two breeding seasons during a year.

University of Michigan

GLOSSARY

Annulus ventralis, an elevation of connective tissue covered by epidermis found between the fifth pair of walking legs of the female. It is used as a sperm receptacle.

Carpus, the fifth segment of the walking leg, counting from the base.

Cephalothorax, the solid front part of the body covered by a continuous chitinous shield. The cephalic groove divides this into an anterior and a posterior section.

Epistoma, the sternal plate lying posterior to the base of the antennae. The anterior process of the epistoma is a projection lying between the bases of the antennae.

Fossa, a cavity, pit or depression.

Merus, the fourth segment of the walking leg, counting from the base.

Obliterated areola, areola limited to posterior and anterior triangular fields by the fusion of the branchio-cardiac lines.

Pleura, the side of an abdominal segment.

Sexual organ, the modified first abdominal appendage of the male.

Truncate, having the terminal edge square or even.

Sinus, an elongated groove.

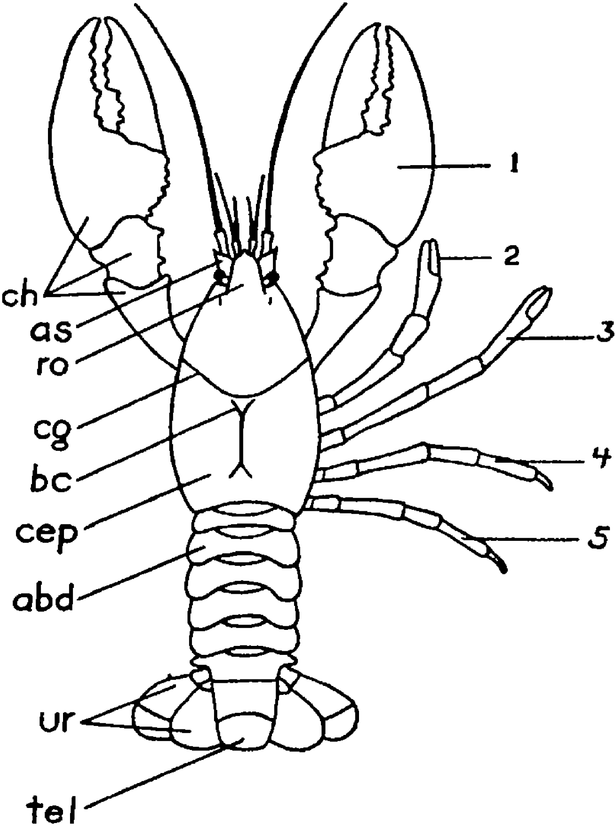

FIG 40 Diagram of *C diogenes*

abd — abdomen
as — antennal scale
bc — branchio-cardiac line
cep — cephalothorax
cg — cephalic groove
ch — cheliped
ro — rostrum
tel — telson
ur — uropod
1–5 — walking legs

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RESPIRATION OF THE HALIPLIDAE (COLEOPTERA) *

JENNINGS R. HICKMAN

INSECTS that live in water are noted for their different methods of securing oxygen. Since the haliplids are primarily aquatic animals, it is of interest to know how they have solved this problem. In fact, several investigators have been concerned with this problem as related to the imagoes, but each has arrived at a different explanation. Matheson (1912, p. 181) concluded that these beetles obtain their air supply by way of the posterior coxal plates — a method quite different from that of the closely allied forms. He thought it was impossible for them to take in air by the tip of the abdomen because the elytra are held firmly in place by special knoblike structures. He failed, however, to observe the fact that they can extend the pygidium far past the tip and at the same time not open the elytra. Brocher (1912, p. 178) announced that these insects take in air in the same manner as do the Dytiscidae. Later on, by means of some experiments and some observations with a magnifying glass, he (1922, pp. 7-17) attempted to prove that his former statement was correct and the view of Matheson wrong. He proposed the explanation that the air store which is noticeable between the posterior coxal plates and the abdomen came from the air store that is above the abdomen and under the elytra, and was hydrostatic only in function. Then Falkenstrom (1928, p. 19) gave an entirely new explanation of the mechanism of respiration and the function of the air store. He stated that under certain conditions the haliplids can take in air as do the Dytiscidae, but that generally they receive enough oxygen from the water by diffusion. The surface of the bubble which is present in the posterior coxal cavity serves as a diffusion membrane. He arrived at

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* Contribution from the Zoological Laboratory of the University of Michigan.

this conclusion after he was unable to see the beetles, under normal conditions, come to the surface of the water to renew the air supply After I had finished my own investigation, Beier (1929, pp 204–209) published his work on *Haliplus wehnckei* Gerh He is inclined to agree with Brocher's explanation, although he gave no experimental evidence for thinking so He thought that the important function of the coxal air store was to allow carbon dioxide to escape from the tracheal system

With these views in mind, I attempted to analyze the method of respiration Many experiments were performed to prove or disprove the views stated above and to add others if necessary The investigation has been directed to answer three questions (1) Where do the beetles obtain enough oxygen to support life? (2) What is the mechanism for obtaining the oxygen? (3) What is the function of the air stores?

The author wishes to express his indebtedness to Professor Paul S Welch, under whose direction this study was made

SOURCE OF OXYGEN

Some aquatic insects obtain their oxygen from that which has been dissolved in water while others take it directly from the atmosphere. According to the work of other investigators, there is a disagreement as to what group the haliplids belong to In order to settle this question, the beetles were subjected to the requirements of both groups and conclusions were drawn from the results

Prolonged submergence experiments

First, the beetles were tested to see whether they could live when they were allowed access only to the dissolved oxygen in the water The following apparatus (Fig 41) was devised for this investigation Two eight-gallon rectangular aquaria (*a*, *a'*) were almost filled with cistern water and placed side by side, one of which was about six inches higher than the other A test tube (*b*) with a pin hole in the bottom and an open glass arm sealed to the test tube about two inches from bottom was inverted in the lower aquarium The arm was connected to a glass tube (*c*) which extended to the bottom of the upper aquarium. Another glass tube led from the bottom of the lower aquarium to the top of the upper aquarium. To the lower end of this tube was connected a glass funnel (*d*). Air was bubbled into the glass funnel and as it passed over into the upper aquarium it carried some water along with it. This maintained the level higher in the upper aquarium than in the lower, and so the water was siphoned back into the test tube and out by way of the pin hole. The test tube contained a wire screen (*f*) suspended so that the beetles could hold on to it and crawl out of the current. Algae (*g*) fastened to the bottom served as a food supply. The beetles were placed in the test tube and allowed to become adjusted before the experiment was started. Then they were submerged. The purpose of the current at the top was to carry away any gas bubbles that might be formed from either the water or the plants. Controls (*h*) were maintained under the same conditions, except that the insects were allowed to get air at the surface. Minimum and maximum temperatures were recorded. *In every case the experimental beetles died in a few days, while the controls lived for weeks.* The accompanying chart (Fig. 42) gives the results at the low temperatures of 4 to 8 degrees. It can be seen that,

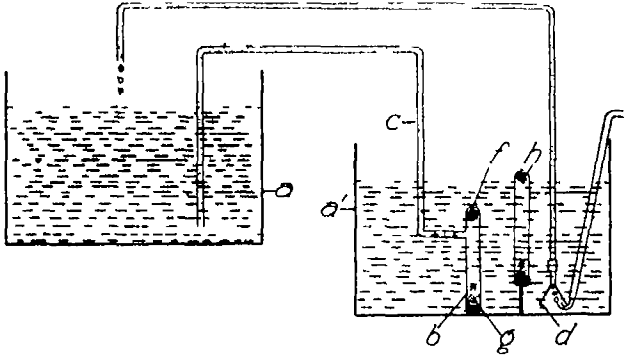

Fig. 41 Prolonged submergence apparatus

though the submerged beetles lived from 3 to 7 days, all the controls lived for 36 days, after which the experiments were discontinued As a precaution to make sure that the beetles were dead, their positions were noted to see whether they moved after a one-day interval When the temperature was raised to 12–15° C, they lived only 1 to 4 days All the controls were alive 24 days later, when the experiment was discontinued When the temperature was approximately 20° C, the submerged insects lived but 18 to 48 hours Controls were alive 30 days later, when the ex-

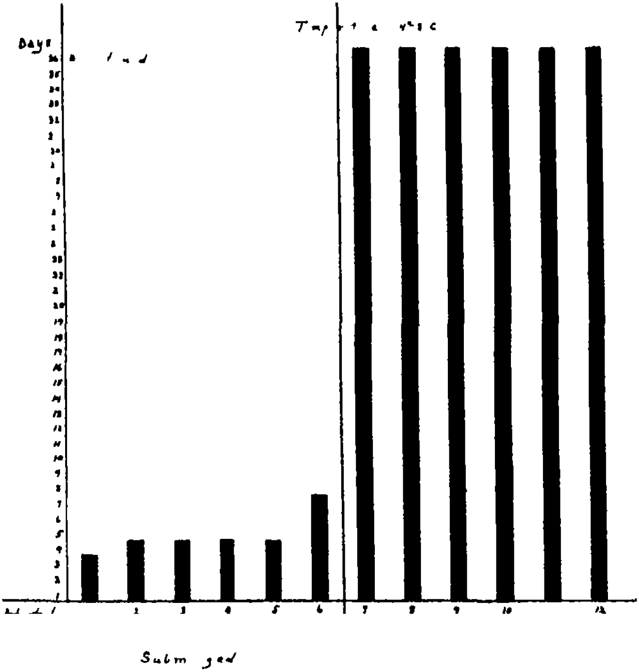

FIG 42 Results of prolonged submergence experiment

periment was discontinued From these results it would seem safe to say that the beetles do not receive enough oxygen from the water to support life even at low temperatures

Surface visits

Since, therefore, the insects could not live when submerged for a long time they must come to the surface to renew the air supply and subsequent observations in the field confirmed this deduction They were seen coming to the surface and diving at times when there were reasons to believe that it was their natural behavior These visits were not frequent, even in small habitats where many beetles were present, but still this same situation prevailed in laboratory cultures, where the beetles had become adjusted The reason for this infrequent surface relation will be explained under the topic "respiratory interval" The field observations are also substantiated by the evidence given under "mechanism"

MECHANISM

Experimental evidence

After it had been found that the beetles renew their oxygen supply by coming to the surface of water, it was important to know by what avenue the air was taken into the tracheae According to other workers, as previously stated, it might be by way of the tip of the abdomen, or by way of the posterior coxal cavity Therefore, in order to determine whether the beetles were able to live when permitted to take in air by one route only, some experiments were performed Since in nature the beetles are at the surface for only a fraction of a second, it was necessary to provide the experimental beetles with the same brief interval if any conclusions were to be drawn as to the way they received their air supply To accomplish this, the following apparatus (Fig 43) was constructed A stiff wire (*a*) with a semicircular bend in the middle was balanced on a standard, having a round, wooden plug (*b*) for a fulcrum On one end of the beam was suspended an open vessel (c) containing an inverted U tube (*d*) One arm (*e*) of the U-tube extended to the outside through a one-hole rubber stopper in the bottom of the vessel, and the other did not quite touch the bottom This was a special device for emptying this vessel of the water which had been led from a tap (*f*) None of the water that slowly dropped in could run out until its level had reached the bend in the U-tube Then it would all be automatically siphoned out before stopping By having the vessel filled and emptied at controlled intervals, that side of the beam would become alternately heavier and lighter, resulting in a fall and rise at regular periods This device is a modification of the Scott-Johnstone siphon bucket The other end of the beam was attached by means of a cord (*g*) to the crank of a shaft (*h*), also made of wire The shaft was supported by two vertical standards (*i*) Between the two supports the shaft had a square bend To this were hung short pieces of wire (*j*) carrying beetles attached at the free end, on small strips of cork, which in turn were submerged in a battery-jar of suitable water They were prevented from floating by means of a sinker (*k*) The beetles were fastened to the cork with very narrow strips of adhesive tape The whole apparatus was adjusted so that, as the siphon bucket was being filled with water, the end of the beam on which it was suspended slowly dropped with corresponding rise of the other end The latter lifted the crank, turned the shaft, and thereby brought the

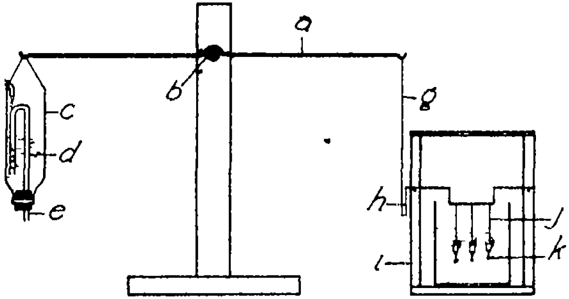

FIG 43 Apparatus for rhythmical exposure of parts of the beetle to the atmosphere

beetles to the surface The apparatus was timed in such a manner that the siphon bucket side of the beam was never down until it was completely filled Then, as soon as a small amount of water had been siphoned off, the beam rose suddenly This timing was necessary in order to make the duration interval of beetles at the surface as short as possible The duration of the submergence interval could also be controlled and varied by allowing the water to enter the vessel at different rates An additional feature was the fact that the apparatus would run day and night with only occasional attention to maintain the water at exactly the same level in the experimental jar Also many individuals could be tested at the same time and all receive identical treatment At first several beetles were attached to the cork so that only the tip of each abdomen extended above the water when raised to the surface It was possible to do this because the coxal plates are shorter than the abdomen, and while the tip was exposed, the coxal plates were completely under water Submergence intervals of ten minutes, thirty minutes and two hours were used In experiments involving each of the intervals, the beetles were alive after two weeks of continuous trial Other experiments already presented showed that they cannot do without air so long The pygidium was observed to be extended into the air each time the beetle was at the surface and, if time permitted, extended and retracted several times Since water prevented the entrance of any air except by way of the tip of the abdomen, it would seem that the experiment definitely proved that the beetles can live if they are permitted to obtain air only in this manner No attempt was made to find the longest possible submergence period, since it had no bearing on this problem Later, beetles were fastened to the apparatus in such a manner that the coxal plates were exposed to the air when raised At the same time, the pygidium was prevented from being extended by means of strips of adhesive tape over the tip The same results were obtained as in the first case Therefore, it can be said from this series of experiments that the beetles are able to obtain air by way of either the tip of the abdomen or the posterior coxal cavity

Photographic evidence

Though close observations under the binocular microscope showed that the beetles broke the surface film with only the tip of the abdomen, nevertheless, there was a possibility that all was not seen, since the duration of this process is very slight For that reason motion pictures of the beetles coming to the surface and diving were taken through the side of the glass vessel In every case the pictures showed only the tip of the abdomen in contact with the air, and the body was not extended far enough to expose the coxal cavity

FUNCTION OF AIR STORE

It is a very noticeable fact that the beetles when submerged have a large bubble extending from the posterior coxal cavity Its function has never been definitely established As stated above, Brocher believed it to be of hydrostatic function only Falkenstrom, although he does not mention the hydrostatic function, adds the idea that it acts as a diffusion membrane and takes in enough oxygen to allow the beetle to live indefinitely submerged, which has already been shown to be wrong In addition, there is the problem whether or not the bubble is a true air store

Hydrostatic function

The beetle reaches the surface by passively floating up or by swimming, but in either case it breaks the surface film with the tip of the abdomen Whenever the bubble is absent, the beetle is heavier than water and will sink Then it can reach the surface only by swimming Orientation is also disturbed, so that it can no longer break the surface film with the tip of the abdomen The same thing is true when the free portions of the coxal plates are removed The clipping of the plates caused some difficulty at first, but with a specially devised instrument it was easily done One tine of a pair of forceps was sharpened to a square edge and bent inward about one half of a centimeter from the end The other tine was also ground down to a fine, square edge and shortened so that the two tips of the tines just met By slipping the straight tine under the coxal plate and pressing down with the other the coxal plate was easily clipped off in bits As little or as much of the coxal plate could be removed as was desired In fact, all traces of the free portions could be removed In order to perform this operation the beetle was held fast by gently pushing its dorsal side down upon adhesive tape Then it was removed to the stage of a binocular microscope, and the tape was held in position by means of the stage clips When a beetle with the free portion of the posterior coxal plate removed is submerged in water, the bubble is no longer present and the beetle's behavior is similar to that of one robbed of its air bubble Its equilibrium is likewise disturbed and it has to reach the surface by swimming Also, it no longer breaks the surface film with the tip of its abdomen, but must crawl out if it is to renew the air supply It would naturally seem that the bubble which the beetle has between the posterior coxal plates and the abdomen helps it to reach the surface and so orients the body that the tip of the abdomen can properly break the surface film It likewise gives some hint as to the function of these greatly expanded posterior coxal plates that characterize this family of beetles

Respiratory function

In order to find out whether the oxygen of the air bubble is used during its stay under water, an analysis was made by means of a modified Krogh s micro-gas analytical method (1908, pp 279 288) A description of the apparatus (Fig 44) and methods used does not seem necessary, since they were very similar to those of Krogh, which are well described elsewhere However, a method of collecting the gas had to be devised It was ultimately found possible to collect the very small bubble with a long flexible, glass capillary tube (*a*) The suction was applied by means of a column of mercury (*b*) When the gas for analysis was being collected, the free end of the capillary tube was placed in the water and allowed to become filled by lowering the column of mercury Then the free end of the capillary tube was brought into contact with the bubble and part or all was drawn into it, followed by some more water Before the bubble reached the end of the capillary tube the column of mercury was raised and the bubble was transferred to the collecting funnel of the analyzer Care was taken to prevent the bubble from being brought into contact with the air and to see that the apparatus was filled with the same kind of water as was in the cultures The bubble could be removed repeatedly without disturbing the beetle The time was noted when the beetle came to the surface and when the bubble was removed The following are a few of the many records taken Results of analyses are expressed in terms of percentage of the whole bubble volume

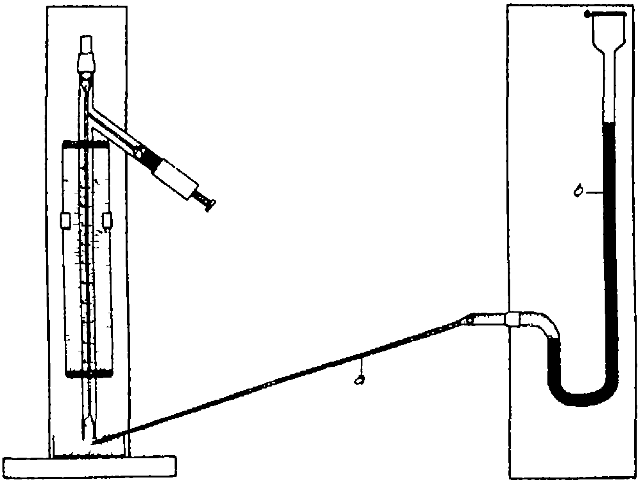

Fig 44 Apparatus for analysis of micro-gas

These percentages are corrected for temperature It is quite impossible to give another explanation of these analyses than this — that the animal during its stay in the water inspires and expires from and into the bubble in the posterior coxal cavity Therefore, the air store is utilised during its stay under water The behavior of the beetle greatly affected the percentage of oxygen present If it had been swimming about very much before the bubble was

TABLE I

ANALYSES OF AIR STORES

Species	Time of analysis	O_2	CO_2
Peltodytes edentulus Lec	Immediately after diving	19 1	0 8
Haliplus triopus Say	Immediately after diving	15 3	0 4
Peltodytes edentulus Lec	Five minutes after diving Active	10 2	1 4
Peltodytes edentulus Lec	Ten minutes after diving Active	5 5	2 3

taken, the percentage of oxygen decreased very rapidly If it had been quiet previous to taking the bubble, the percentage of oxygen was much higher These things have to be taken into account in order to get a clear understanding of what becomes of the oxygen

Respiratory movements

If the oxygen of the air store was used by the beetles, there should be respiratory movements under water As regards this, the author believes he has proof that such movements occur After careful observations under the binocular microscope, the attached bubble was seen to become smaller and larger at rhythmic intervals This change in volume of the bubble is interpreted as a sign of respiratory movements Reasons for this statement are as follows On examining a beetle out of water, with its elytra removed, there are very evident movements of the dorsum that would be taken as respiratory movements from what is known about other insects Such movements under water would cause the bubble to become smaller and larger, as was observed With the contraction of the dorsum, the space under the elytra would become larger and the air in the bubble would come in to fill it On expansion of the dorsum the space would become smaller and then the air would be forced out Since the beetles were at rest when observed, no other explanation can be given for this noticeable change in volume that occurs in the bubble

Respiratory interval

When beetles are first put into the aquaria, they are always quite active and come to the surface very frequently The same thing is true when they are disturbed, after they have become adjusted to an aquarium, or to natural conditions It is very obvious that increased activity on the part of beetles requires more oxygen and therefore more frequent trips to the surface are necessary to supply this need The duration of the submergence intervals of a disturbed beetle varies irregularly from two to three seconds to several minutes On examining good cultures, however, a very noticeable difference is observed from what has been previously stated The beetles are not very active, but move occasionally about the vegetation, now and then swimming short distances When the proper precaution was taken, some were observed to remain submerged continuously for more than two hours No attempt was made to find the longest period that an individual would remain submerged when not disturbed It would seem from these two contrasting observations that these insects ordinarily use little oxygen and, therefore, frequent trips are not necessary to supply their needs When they are disturbed and swimming about, the oxygen need is much greater and the submergence interval is, therefore, shorter

SUMMARY

1 The imagoes of the Haliplidae must come to the surface of the water for their air supply even when the temperature is about zero Centigrade

2 Normally, they take in air by way of the tip of the abdomen, although they can live if permitted to obtain the air only by way of the posterior coxal plates

3 The air store retained by the posterior coxal plates has both respiratory and hydrostatic functions

4 The duration of the submerged interval is dependent upon the nature of their activity

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INCREASED GROWTH IN HYBRID SUNFISHES

CARL L. HUBBS AND LAURA C. HUBBS

WE TAKE in nature a considerable number of sunfishes, which we have interpreted as intergeneric hybrids, especially as between *Apomotis cyanellus*, the green sunfish, and *Eupomotis gibbosus*, the pumpkinseed. We have by actual experiment validated this interpretation, for the hybrid combination specified, and also for the *Apomotis* × *Helioperca* cross (Hubbs and Hubbs, 1930).

In some natural waters in Michigan, the largest sunfishes we have taken are hybrids. The largest one from Third Sister Lake, near Ann Arbor, is an *Apomotis* × *Eupomotis* cross. By far the two largest taken in Sunken Lake, in Presque Isle County, are apparent *Eupomotis* × *Helioperca* hybrids. The latter show probable hybrid vigor also in their excessive development of secondary sexual characters.

We have been able to put this suspected increased growth of hybrid sunfishes to a number of tests. We have studied the growth of *Apomotis*, *Eupomotis* and hybrids between these genera, in nature, in Wiard's pond, near Ypsilanti (see Fig. 45). Material of all three from this pond has been brought into the Experimental Aquarium of the Museum of Zoölogy, during their first winter, and has been kept there for a year under conditions as nearly uniform as possible for all (see Fig. 46). Finally, we have maintained our experimentally produced hybrids of *Apomotis* × *Eupomotis*, and have measured their growth to the end of their first year. All the measurements, about 1200, were carefully taken on living fish from tip of snout to end of vertebral column, by means of dividers. The data are presented in Table I and in the graphs.

We cannot be sure whether the hybrids taken in nature are in the first generation. Some, from their appearance and from

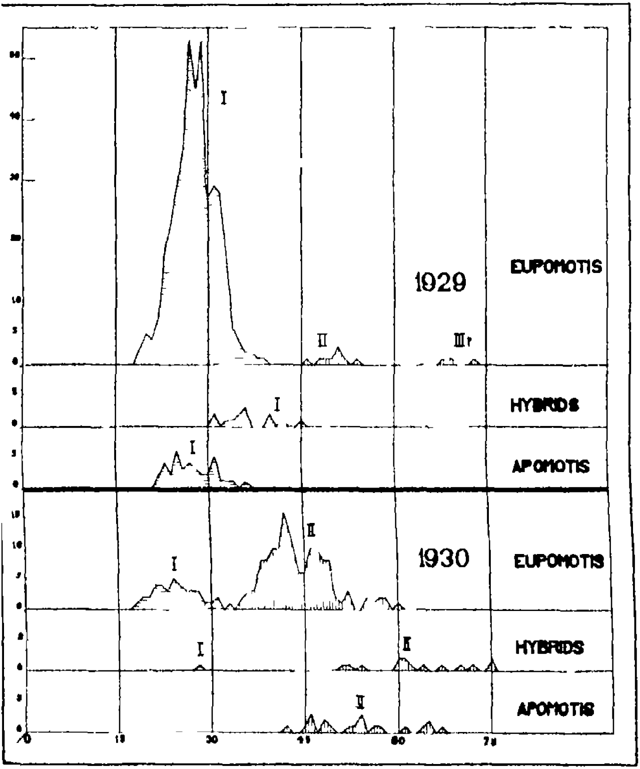

FIG 45 Size frequency graph for two genera of sunfishes, and of hybrids between them Material collected before start of spring growth, in Wiard s Pond, Michigan

the ecological conditions, we suspect may be backcrosses of the hybrid with *Eupomotis*

The samples for measurements were all taken in February and March, when none of the fishes from the pond near the end of

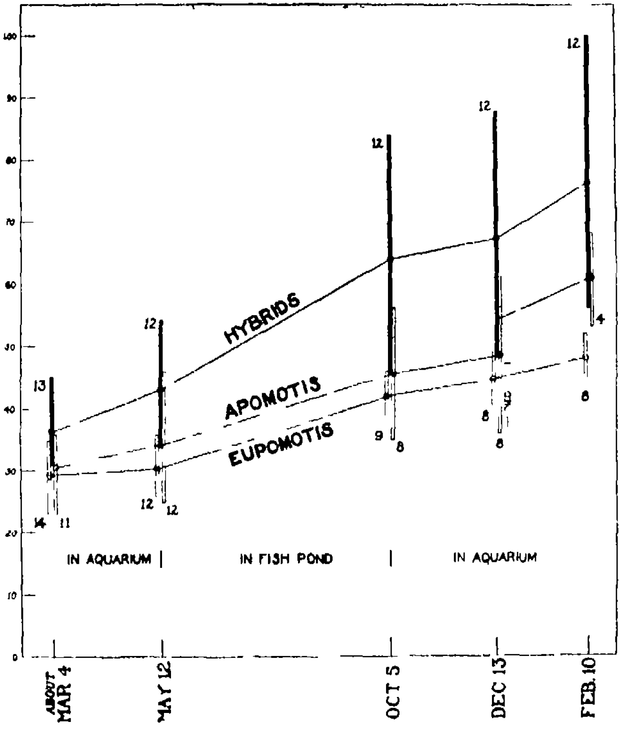

Fig 46 Graph showing observed growth of two genera of sunfishes and of hybrids The lines indicate the range in size at each date for each lot, the circles show the average size for each

their first or second year had started to grow (scales for the 1930 sample only examined), because none had formed an annulus at the scale margin (see Creaser, 1926) Their measurements are therefore finely comparable A few of the older fish showed a little growth outside the previous winter mark, but whether the small growth indicated had taken place in the latter part of the winter or during the whole previous growing season was not clear, nor does this difficulty seriously interfere with our comparisons (see item 10 of Table I) None of the first- or second-year fish, of all the 207 taken in 1930, had scale characters which admitted of any doubt whatever in their indication of the age of the fish Furthermore, the age-determinations from scale readings are well confirmed by the size-frequency distribution (see Fig 45) The first year-group for the 1929 samples stands out so well by frequency distribution that age-determinations by the scale method (Creaser, 1926) were not considered necessary

For the second year-group taken in February, 1930, we computed the first and second year's growth, on the widely used assumption that scale growth to each winter mark is proportionate to the growth of the fish for the corresponding period The computation made by direct proportion, uncorrected, involves errors (Creaser, 1926), but these are probably in the same direction for all three sets The fact that the values for the computed growth during the first year, 1928 (item 1 of Table I), are lower than the measured growth for the same period (item 2), is probably an expression of the error in the method of growth computation The value for the second year's growth in 1929 (item 5) is the difference between the computed first year's growth and the measured growth for the first two years

The first full year's growth of the aquarium-bred hybrids (item 4) was greatly in excess of the first season's growth of the natural hybrids, although all were measured in February and March (the former on February 15) This is probably to be explained by the facts that the laboratory hybrids were hatched long before natural spawning and grew over the winter

The growing of the hybrids and of the parent species under controlled conditions (items 6 and 9 of Table I, and Fig 46) was carried out with considerable care The specimens, uniformly nearly one year of age (all had completed their first growing season), were brought into the Experimental Aquarium from Wiard's pond in February and March, 1929, and kept together in a large aquarium until summer, when all were put into a garden fishpond. In the early fall they were returned to the aquarium and kept together until some of the hybrids had grown so much larger than the examples of the parent species that they started to devour them. The fishes were then sorted by size into two adjacent aquaria and given similar treatment. When in the aquarium these fishes were fed all the food they would take, so as to insure the filling of the smaller ones. The bulk of the food consisted of bird meat, which is a very satisfactory growth food for sunfishes. This was frequently varied by living food (earthworms, etc.) and other matter, even through the winter. Care was taken to give all the individuals as nearly optimum conditions as possible. Nevertheless, the hybrids grew about twice as fast as the *Eupomotis* sample, and much faster than the *Apomotis* specimens.

The difference between the first year's growth of the hybrids and of *Eupomotis* in 1929 was probably greater than indicated in item 3 of Table I, because the one hybrid of that year-group taken was very badly parasitized, and probably stunted down to a size approaching that of *Eupomotis* at the same age.

The greater growth of the hybrids is suggested also by the size of the three oldest sunfishes caught in February, 1930. The only three-year hybrid (with 2 annuli, not counting the one at margin) taken was 107 mm. long. Two five-year pumpkinseeds were only 114 and 118 mm. long, and a seven-year green sunfish, only 4 mm. longer than the three-year hybrid.

Table I shows only the data and the mean sizes with the probable error of each mean, so far as computable. Table II indicates the consistent excess in growth of the hybrids over that of each parent species for the same life-stages. This excess in growth varies from 7 to more than 100 per cent. The mean per cent excess of growth in length of the hybrids, weighted by the statistical probability of significance of the determinations, is 50 per cent over that of *Eupomotis* and 36 per cent over that of *Apomotis*. The mean for the excess in growth of the hybrids, derived from the determinations of the entire growth to the given stage (with the three sets of determinations, for the second year's growth or for the second winter's growth eliminated), is about

TABLE 1

COMPARATIVE GROWTH OF *Eupomotis*, HYBRIDS AND *Apomotis* FOR CORRESPONDING STAGES IN LIFE HISTORY

Growth stage	Genus	Measurements to nearest five millimeters																						No	Mean	PE_M
		0	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100	105			
year's growth in pond in computed from scale mea- nts of fish in second winter	Eupomotis				17	45	54	16	1															133	23	0.3
	Hybrids					3	4	1	5	1														14	29	1.2
	Apomotis					2	11	6		1														20	27	0.6
t year's growth in pond in 1928 measurements of yearlings in first winter	Eupomotis					10	156	18	31	2														392	28	0.1
	Hybrids							–		3	1													13	36	0.8
	Apomotis					2	19	13	1															35	27	0.3
First year's growth in pond in 1929 measurements of yearlings in first winter	Eupomotis					13	18	7	1															39	24	0.4
	Hybrid							1																1	28*	
rst year's growth of aquarium- ed and reared hybrids (Feb 29 to Feb 1930)	Hybrids								1	7	9	4	4	6	5	1	3				1			41	54	1.3
Second year's growth in pond in 1929 computed from scale measurements of fish in second winter	Eupomotis			2	12	76	31	11	1															133	22	0.3
	Hybrids					1		5	4	3	1													14	34	1.0
	Apomotis					3	7	5	4	1														20	28	0.8

TABLE I (*continued*)

Growth stage	Genus	Measurements to nearest five millimeters																						No	Mean	PE_M
		0	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100	105			
6 Second year's growth in aquaria (about March 4 to Dec 13 1929) following first year in pond	Eupomotis																							8	15 6*	
	Hybrids																							12	30 7*	
	Apomotis																							8	17 7*	
7 Second winter's growth in aquarium Dec 13 1929 to Feb 10 1930	Eupomotis																							8	3 5*	
	Hybrids																							12	8 9*	
	Apomotis																							4	6 5*	
8 First two years growth in pond measurements of fish in second winter (Feb 1930)	Eupomotis								8	52	43	22	5	3										133	44	0 3
	Hybrids											3	1	5	2	2	[illegible]							14	63	1 4
	Apomotis									1	4	4	6	1	4									20	54	1 1
9 Two years growth the first (1928) in pond the second (to Dec 1929) in aquaria	Eupomotis									3	4	1												8	44	0 8
	Hybrids											3	2		1	1	1	[illegible]	1	1				12	67	[illegible]
	Apomotis								1		3	2	1	1										8	49	1 [illegible]
10 First three or four years growth of *Eupomotis*, compared with first three years growth of hybrid in pond	Eupomotis													1	7	4	7	1	2	4	1			27	75	1 3
	Hybrid																						1	1	107*	
		Total number of length determinations or computations																						1130		

* Mean based on actual measurements to nearest millimeter

TABLE II

EXCESS IN GROWTH OF HYBRIDS OVER THAT OF PARENT SPECIES FOR THE SAME LIFE STAGE

Excess over *Eupomotis*		Growth stage (Rows numbered as in Table I)	Excess over *Apomotis*	
Percentage	$\frac{M_H - M_E}{PE_{(M_H - M_E)}}$		$\frac{M_H - M_A}{PE_{(M_H - M_A)}}$	Percentage
26	5	1 First year pond 1928 computed	1 5	7
29	10	2 First year pond 1928 measured	10	33
17 *	ca. 1 5 †	3 First year pond, 1929 measured		
55	12	5 Second year, pond, 1929 computed	5	22
103	ca 5 ‡	6 Second year aquarium, following first in pond	ca. 6 ‡	74
154	ca 1 ‡	7 Second winter aquarium following No 6	ca. 2 ‡	37
43	13	8. First two years pond measured	5	17
54	8	9 Two years first in pond second in aquarium	6	37
43	ca. 5 †	10 Three or four years, *Eupomotis* as compared with three years for hybrid		
50		Mean percentage of excess of growth in length of hybrids over that of parent species weighted by times differences between means are greater than probable errors of difference		36
41		Mean for excess of growth in length of hybrids over that of parent species, derived from determinations of entire growth to given stage (three series, Nos. 5 to 7, for second year's or second winter's growth eliminated)		29
180		Mean greater growth of hybrids in weight as compared with parent species (rough estimate) §		115

NOTES TO TABLE II

* Value too low, because the one yearling hybrid caught was very badly parasitized

† Value computed on assumption that standard deviation for size of hybrids is the same as for the *Eupomotis* sample The possible error thus involved would not greatly influence the final averages.

‡ Value computed on the assumption that the probable errors of the averages are the same as for the total lengths of these same fishes at the end of their second year (No 9) The error thus involved would not greatly modify the final average, and would enter only *into* the first of the three final averages computed.

§ The mean greater growth of the hybrids in weight as compared with the parent species, was determined on the following essentially valid assumptions that the mean for excess in growth in length to end of given stages is correct that weight increases in proportion to the cube of the length in each species, and that all the fishes average not far from the same in weight for each length that the lesser depth of *Apomotis* is about compensated for by their greater thickness, that the hybrids are intermediate in both depth and thickness

41 per cent over that of *Eupomotis* and 29 per cent greater than that of *Apomotis*. From these latter figures we have estimated, with no very large probable inaccuracy, the mean greater growth of the hybrids in weight, on certain warranted assumptions indicated in the last footnote (§) of Table II. The growth in weight of the hybrids was roughly 180 per cent greater than that of the *Eupomotis* samples, and 115 per cent greater than that of the *Apomotis* samples.

The increased growth of the intergeneric sunfish hybrid *Apomotis cyanellus* × *Eupomotis gibbosus* may, therefore, be regarded as established. It remains to be determined to what degree this increased growth-rate persists in further generations, if the hybrids are fertile. It also remains to be learned whether the increased growth-rate of this and perhaps of other hybrid combinations may have any significant bearing on pond fish culture.

ADDITIONAL DATA

As the paper was going through the press, some additional evidence on the increased rate of growth of hybrid sunfishes of the *Apomotis-Eupomotis* combination was obtained.

A third sample was taken in Wiard's Pond, Michigan, on November 23, 1930. The average size of the young hybrids, on this date not quite one year old, was again found to be greater than that of either parent species. The difference, however, was not very great, but was of probable though not certain "statistical significance."

Lengths (to caudal fin) of 61 young of *Eupomotis* 20 to 39 mm., average 28.40 ± 0.38 mm.

Lengths of young of 13 hybrids, 27 to 38 mm., average 30.76 ± 1.285 mm.

Lengths of 39 young of *Apomotis* 18 to 41 mm., average 26.82 ± 0.66 mm. (All measurements on young taken on preserved specimens.)

Difference between means for hybrids and *Eupomotis*, 2.27 mm., which is 1.7 times the probable error of the difference.

Difference between means for hybrids and *Apomotis* 3.94 mm., which is 2.7 times the probable error of the difference.

The single 2½-year-old hybrid taken on November 23 was 100 mm., much larger than any of the parent species of the same age. Seventeen of *Eupomotis* were 53 to 77 mm. long and averaged 67.7 mm.; two of *Apomotis* were 74 and 82 mm. long. A 3½-year-old sunfish (*Eupomotis*) was 91 mm. long, and one 4½ years old was 108 mm. long.

Young sunfishes of the same two species and of hybrids between them were also taken in Phoenix Pond, near Plymouth, Michigan, November 13 to 22, 1930. The hybrids were again found to be larger than either parent species. The results as conventionally computed show a statistically significant difference in the size, but since only four hybrids were obtained, they cannot be regarded as more than confirmatory of the results obtained on fuller material.

Lengths (to caudal fin) of 396 young of *Eupomotis*: 20 to 44 mm.; average, 31.29 ± 0.14 *mm.*

Lengths of 4 hybrids: 35 to 39 mm.; average, 37.25 ± 1.66 mm.

Lengths of 48 young of *Apomotis*: 21 to 40 mm.; average, 29.98 ± 0.40 mm. (All measurements taken on preserved specimens.)

Difference between means for hybrids and *Eupomotis*: 5.96 mm., which is 3.6 times the probable error of the difference.

Difference between means for hybrids and *Apomotis*: 7.27 mm., which is 4.3 times the probable error of the difference.

University of Michigan

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THE COREGONID FISHES OF NORTHEASTERN AMERICA

WALTER KOELZ

FOREWORD

THIS paper embodies further studies of the coregonid fauna of the Great Lakes area and is, therefore, an extension of an earlier paper (Koelz, 1929). Much of the work was done while I was holding the Alfred H. Lloyd Fellowship during the year 1928–29, and it is hoped that the results may be found in some degree worthy of the opportunity the University of Michigan afforded in granting the fellowship. The investigation was completed while I was serving as ichthyologist in the Institute for Fisheries Research.

It may appear to some that forms have been needlessly multiplied, but anyone will readily find by consulting the literature pertaining to these fishes that other workers have almost uniformly set up species much more freely than subspecies have been made here. Many of these species are not here recognized as worthy of even the minor designation. It is, after all, a matter of lesser moment in what manner the morphological forms are designated. The naming of a form merely calls attention to peculiar characteristics and affords a convenient *means of reference*. The *understanding* of the significance of the phenomena thus labeled is one of the great aims of biological investigation.

The types of all the new forms described are in the Museum of Zoölogy of the University of Michigan. Paratypes, unless otherwise indicated, are preserved there also. In addition, the Museum usually has at least one specimen of the race of each coregonid found in the various lakes here reported on.

Individuals and institutions have generously made available most valuable material and I acknowledge my obligation to

Mr J R Dymond of the University of Toronto for the loan of his collections, to Mr John R Greeley of Cornell University and Professor E H Eaton of Hobart College for the loan of the collections made under the New York State Conservation Department Surveys, to Professor John N Lowe of the Michigan Northern Normal College for special collections of valuable material, to Mr H H MacKay of the Ontario Game and Fisheries Department for allowing me to examine the specimens in the Department's collections, to Professor George Wagner of the University of Wisconsin for the use of the vast coregonid collections of the Wisconsin Natural History Survey, and to the authorities of the U S Bureau of Fisheries, U S National Museum, Field Museum of Natural History, and the Museum of Comparative Zoology for the loan of their coregonid collections

GENERAL REMARKS

These studies are based on an examination of over 2122 specimens of *Leucichthys artedi* from 119 lakes, 13 of *Leucichthys bartletti* from the type locality, 294 of *Coregonus clupeaformis* from 42 lakes and rivers, and 41 of *Prosopium quadrilaterale* from 9 lakes The material of *L artedi* came from Michigan, Upper Peninsula, 17 lakes, 565 fish, Michigan, Lower Peninsula, 26 lakes, 597 fish, Wisconsin, 29 lakes, 555 fish, New York, 11 lakes, 75 fish, Indiana, 4 lakes, 10 fish, Minnesota, 2 lakes, 4 fish, Ontario, 25 lakes, 279 fish, Manitoba, 2 lakes, 23 fish, Saskatchewan, 2 lakes, 9 fish, Alberta, 1 lake, 5 fish The specimens of *C clupeaformis* originated as follows Michigan, Upper Peninsula, 5 lakes, 82 fish, Michigan, Lower Peninsula, 2 lakes, 31 fish, Wisconsin, 2 lakes, 74 fish, New York, 9 lakes, 33 fish, Maine, 10 lakes and rivers, 43 fish, Montana, 1 lake, 6 fish Minnesota, 1 lake, 3 fish, New Hampshire, 1 lake, 1 fish, Ontario, 9 lakes, 25 fish, Saskatchewan, 3 lakes and rivers, 8 fish The specimens of *P quadrilaterale* are from Maine, 2 lakes, 12 fish, New York, 5 lakes, 27 fish, and New Hampshire, 2 lakes, 2 fish

Not all available characters have been studied in making analyses of the specimens Through long experience with Great Lakes forms it has been found that certain structures are extremely variable (adipose fin) or else very constant (fin rays, branchiostegal rays) or even impossible of accurate recording (body width), and therefore time has not been given to a study of such characters Food has not been examined, partly because Great Lakes studies indicate that the species there eat what is available, and no ecological data have been employed, chiefly for the reason that none are recorded Most of the specimens have been accumulated in the course of casual collecting and data on the distribution of the species in the lake of origin have not been gathered Time of spawning is not discussed in the accounts of the various forms, partly because there is generally no clue to the date of egg-laying other than the sexual condition of preserved specimens and partly because the breeding season has been found in Great Lakes forms to be extremely variable, differing from season to season, from lake to lake, or even from school to school in the same locality There is, however, no reason to believe that any of the inland lake forms, with one exception, have breeding habits different from those of the known races of related forms in the Great Lakes (See Cahn, 1927, for an account of spawning of *L artedi* in inland waters)

It was pointed out by Koelz, 1929, that the coregonids are a variable group In most of the species isolated populations exhibit more or less pronounced structural differences, and these intraspecific differences may be greater than those which separate one species from another, especially in the genus *Leucichthys* Furthermore, certain of these variants may resemble another species of *Leucichthys* much more closely than they resemble any of the other forms within their species group The species *Leucichthys artedi* was shown to be the most variable of the genus

Where there are intergrading forms in intervening areas, the relationship of these very different intraspecific variants can be demonstrated, and in the Great Lakes, where all the habitats are connected, such intergradation has been established In inland lakes, however, isolation is for the most part complete and intergradation cannot then be shown, except that forms, selected it may be from areas that are widely different in their geological and biological history, might be found to fill the gap between extreme types of variation The construction of a table of relationships is of course always open to objections in a group like *Leucichthys*, in which the species are very similar and extremely variable, but in this paper I have treated any form of *Leucichthys*, when only one species occurs in a given body of water, as a member of the *artedi* group

My reasons for doing this are based on facts of (1) distribution and ecology and (2) structure (1) *Leucichthys artedi* has the widest distribution of the genus in the Great Lakes It occurs in all the lakes Of the other eight species none occurs in Lake Erie, a body of water which on account of its shallowness is probably closer in its environmental conditions to inland lakes than the other deeper or larger bodies of the great chain *L artedi* is abundant in all the lakes, keeping in all but Erie and Ontario principally to depths of less than 20 fathoms, but traversing freely the surface layers, even over great depths The species is known to occur abundantly in Lake Erie in its greatest depths (35 fathoms) and in Lake Ontario to about 60 fathoms Lack of competition may have opened these deep waters to a species that is apparently very adaptable

(2) There is a unity of appearance in all these inland-lake forms They all look most like *L artedi* This appearance is more or less indefinable, but it is none the less real There are slight differences of shape, flesh texture, color, etc , that distinguish the various species of *Leucichthys* found in the Great Lakes, and anyone familiar with the nine species can identify by inspection the majority of individuals I have on occasion had fishermen select collections of a given species from a mixed catch and have found them able to make identifications without resorting to the aid of measurements or counts In addition to general appearance, the regularly applied body proportions and counts of multiple parts of the various inland-lake races are not as a rule much different from those of races of *L artedi* from the Great Lakes Probably only in the case of the forms *birgei*, *wagneri*, and possibly *greeleyi* would anyone feel that the relationships are in doubt, and anyone of this opinion may call these forms species of *Leucichthys*, rather than subspecies of *L artedi*, for it is not at all clear that they are related to any of the deep-water forms

The specimens of *Leucichthys artedi* may be divided into 24 groups, those of *Coregonus clupeaformis* into 7, and the *Prosopium quadrilaterale* into 2 The characteristics of the first two are shown in the analyses on pages 311–313 and 371 The division is, of course, purely arbitrary In most cases a form is distinguishable from any other by exhibiting average differences in at least two characters It is purely the result of chance if this is so, because as a matter of procedure I believe any form is worthy of a name if it can be shown to exhibit certain constant, even if only average, differences, in a single character The application of a name has nothing to do with the meaning of the phenomena so ticketed The significance of such differences cannot be determined without further investigation and may even remain incomprehensible, but the name serves to call attention to the differences

Not all of these forms have been found to be equally abundant In the species *L artedi* typical *artedi* has the widest distribution, and outside the Great Lakes is known to occur in 19 inland lakes *Wagneri*, *hankinsoni*, *magnus*, *osmeriformis*, *birgei* and *microcephalus* are known only from the type locality The rest are known from a varying number of lakes *clarensis* 20, *mackayi* 13, *sisco* 11, *woodi* 7, *greeleyi* 7, *clemensi* 6, *tullibee* 6, *winnipegosis* 6, *russeli* 3, *huronicus* 3, *sargenti* 3 *lowei* 2, *mendotae* 2, *atikamek* 2, *annensis* 2, *albus* 1, *manitoulinus* 1

In *Coregonus clupeaformis* typical *clupeaformis* is known to occur nowhere outside the Great Lakes, except in Torch Lake *Neo-hantoniensis* is found in 22 localities, *gulliveri* in 5, *stanleyi* in 5, *latus* in 1, *dustini* in 2, and *medorae* in 1

Probably no two of the isolated races that have been grouped under any one of these names are, in fact, exactly alike The values of most of the systematic characters employed to separate the forms change with growth, and the races cannot be compared in more detail until sufficient comparable material is available The data at hand show merely that the races grouped under a given name resemble one another more closely than races of a different name

The distribution of the various races only roughly follows geographical areas The variants of *L artedi* may serve as a basis of discussion In general, the fish of the southern part of the range in Michigan, Indiana and Wisconsin belong to a short-headed form *sisco* that is distinguished from the typical form by having also a short snout and maxillary However, in a lake in the Upper Peninsula of Michigan there is found a race *microcephalus* still more extreme in these characters Typical *artedi* seems to occur in the belt above the *sisco* zone in Wisconsin and the Lower Peninsula of Michigan and sporadically east to Lake Champlain A poorly differentiated variant *osmeriformis* is found in Seneca Lake, New York In northern Wisconsin there occurs *clarensis*, a race that is like typical *artedi*, except in having a proportionally shorter snout and maxillary, and similar specimens are found in a few lakes in southern Michigan In the Upper Peninsula of Michigan there occur chiefly forms that are like the race *clemensi* in Lake Nipigon, such are also found in one lake of northern Wisconsin very close to the type locality of *clarensis* There are also in this area several forms that have differentiated both from the *clemensi* type and from the *greeleyi* type, *russeli*, *atikamek*, *huronicus* and *annensis* The first occurs also in Ontario, and probably in New York, the second in northern Wisconsin, the third probably also on Isle Royale and in New York, and the last probably also in Ontario *Greeleyi* occurs in the deep lakes in the Lower Peninsula of Michigan and New York, but it does not occur in all the deep lakes in these places The *albus* form occurs outside the Great Lakes in an inland lake of Ontario The deep-bodied races, *tullibee winnipegosis*, *magnus*, *manitoulinus* and *woodi*, seem to be northern in their distribution, occurring from the northern half of the Lower Peninsula of Michigan northwestward through northern Wisconsin, to Minnesota, to the plains provinces An extreme *tullibee* type, however, differing but slightly, occurs in New York, far east of this given range (*hankinsoni*)

If the distribution of the morphological forms is considered on the basis of certain characteristics alone, as, for example, deep body, there is even less satisfactory regional distribution The forms with deepest bodies occur in the prairie provinces, but in New York in the midst of a belt of terete races and here and there between are found forms as deep-bodied as the most extreme ones known from the northwest (Number of lateral line scales and fin length seem to be associated with body depth, the deepest fish having generally fewest scales and longest paired fins) Gillraker number seems to be reduced in deep-water lakes, except that the form from Seneca Lake (618 feet deep) has more than the typical *artedi*, with which it is otherwise identical, and in Lake Nipigon (over 350 feet deep) the number is not reduced The gillraker number is also reduced in forms that inhabit lakes not particularly deep (Anne, Oneida) Short-headedness might be considered a southern trait if the shortest-headed form of all were not known from the Upper Peninsula of Michigan It does seem that the fish which are found in the northern lakes have longer fins, but this short-headed fish of the Upper Peninsula is also one of the shortest-finned forms

Facts of geological history do not contribute much to an understanding of the distribution of these forms The region in which the lakes under study lie was covered in large part or *in toto* by the last ice-sheet, and it is not probable that these lakes retained any of their fish fauna during the last ice advance Of course this fauna may have been differentiated previous to the last ice advance and the population driven ahead of the ice into waters of various river systems, now distinct but then connected The nine Great Lakes forms, unless they came in from the northwest at a late stage of the Great Lakes, must have been thus exiled and undoubtedly often in company with at least some of these hypothetical pre-Wisconsin inland-lake inhabitants, and it requires elaborate postulation to account for the fact that these numerous closely related stocks maintained their identity during the adjustment of the water levels after the ice retreat It is also possible that from a complex stock segregation of peculiarly adapted populations is taking place in the various localities There seem to be few facts to present in this connection and there is nothing to be settled by speculation

Koelz, 1929, has pointed out that latitude is not so important a factor in the distribution of aquatic forms as of terrestrial ones, since conditions in lakes depend on their depth, the form of their basin, etc, so that two lakes side by side may be totally different in their physical features, and lakes in high latitudes may resemble closely, at least in many features, those in lower latitudes The study of the environment that different water bodies offer may then throw light on the distribution of the various morphological forms Such an environmental study should be made, however, with direct reference to the fish problem The need of hydrographic studies in relation to aquatic biology has been expressed often, but such researches have generally been carried on quite without regard to any particular biological problem, and consequently we often lack the data that are most needed It is understood, for example, that the most critical time in the life-history of the fish is during its early development, its somatic structures are moulded then and the mortality rate is highest, and it is, therefore, most important to know what the environmental conditions are during that critical period[1] Experiments have shown that great aberrations can be produced in the nature of the embryo if the "normal" environment is altered in the matter of temperature, chemical constitution and so on We know also that, after hatching, somatic structures can be radically altered by the environment as well as by character and quantity of food and similar things An understanding of the evolution of the various coregonid forms must then wait on studies of environment, coupled with breeding and rearing experiments It is conceivable, finally, that the operative factors that produce these differences are so minute as to escape our present methods of analysis

If the inclusion of all these forms within the species group *artedi* is accepted, it is permissible to discuss the correlation of systematic characters, but here again it seems to be possible to make no laws In general deep-bodied forms have few lateral line scales Lesser Slave Lake fish are among the deepest-bodied races of the series and yet are only intermediate in scale number Long fins seem to be associated with deep-bodiedness, but the Oneida Lake race has the deepest body of any known race and in the matter of fin length stands intermediate. Deep-bodied forms in general seem to be long-headed, but the Gogebic Lake race, with the shortest head of all, is intermediate in body depth. Relative lengths of snout and maxillary, as well as gillraker number, fluctuate without obvious relation to other body parts. With high and low values for eight characters, L/H, H/S, H/M, PV/P, AV/V, L/D, lateral line scales and gillrakers, it is theoretically possible to have 256 forms. Only 24 have been discovered and it is likely that many of these characters are linked together.

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[1] I should like to mention here what the geneticist who deals abundantly with eggs and seeds soon realizes but what has so far it seems escaped the fish culturist, namely, that many zygotes lack the capacity to develop to the adult stage They perish either in embryonic development or in the early post-embryonic stages, and therefore the percentage of potential survivors can never be more than a fraction of the initial supply of fertilized eggs.

SPECIES OF COREGONIDAE

Leucichthys artedi (Le Sueur)

The type locality is Lake Erie and Lake Ontario. The type is not extant. Of the two forms that occur in these lakes Koelz, 1929, has restricted the name to the slender one. A closely similar form is found in the other Great Lakes, and in view of the facts that relatively very few of typical *artedi* are known from the type locality and that in the publication cited above the characteristics of these specimens are shown to be nearly like those of Lake Michigan specimens, for which there are available numerous analyses, the Lake Michigan form is used here as the representative of typical *artedi*.

ANALYSIS OF THE SUBSPECIES OF *LEUCICHTHYS ARTEDI*

A^1 Gillrakers on the first branchial arch usually more than 39 and fewer than 46, lateral line scales nearly always more than 72, L/D nearly always more than 4.1.
  B^1 PV/P usually more than 1.6, L/D in fish under 200 mm. usually more than 4.5.
    C^1 L/H in fish under 215 mm. usually less than 4.3.
      1. H/S less than 4.1 *greeleyi*
      2. H/S 3.9–4.2 *huronicus*
    C^2 L/H in fish under 215 mm. usually 4.3 or more.
      3. H/S 3.8–4.1 *annensis*
  B^2 PV/P usually less than 1.6. L/D in small fish less than 4.5.
      4. Eye large *sargenti*

A^{2} Gillrakers on the first branchial arch usually more than 41 and fewer than 48, PV/P usually more than 1 5 and less than 2 1, body deep (except *mackayi*)

B^{1} Scales usually fewer than 70, L/D less than 3 4

5 H/M usually over 2 9 *hankinsoni*

B^{2} Scales usually more than 70

C^{1} L/D more than 3 3 but in fish over 225 mm usually less than 4, in fish under 200 mm usually less than 4 5

D^{1} H/S usually less than 4 1

6 H/M usually less than 2 8, AV/V usually 1 3–1 5 *birgei*

7 H/M usually more than 2 7, AV/V usually 1 5–1 7 *russeli*

D^{2} H/S usually over 4

8 H/M usually 2 7–3, AV/V usually 1 4–1 6 *atikamek*

C^{2} L/D in small fish usually over 4 5

9 H/S about intermediate between D^{1} and D^{2} *mackayi*

A^{3} Gillrakers on the first branchial arch usually more than 45

B^{1} Body slender, L/D usually more than 4

C^{1} PV/P usually more than 1 8 in specimens over 200 mm long

D^{1} H/M usually 2 7–3, H/S usually 3 7–4

10 Gillrakers usually 46–51 but frequently fewer *artedi*

11 Gillrakers usually 47–51, but often more *osmeriformis*

D^{2} H/M usually 2 9–3 1, H/S usually 3 9–4 2

12 Otherwise about as 10 *clarensis*

C^{2} PV/P usually less than 1 9, H/S 3 7–4, H/M 2 7–2 9

13 Scales usually 71–76, gillrakers usually 46–49 *clemensi*

14 Scales usually 76–86, gillrakers usually 48–52 *lowei*

B^{2} Body deep, L/D usually less than 4, except for *sisco*

C^{1} Paired fins short, PV/P usually more than 1 8

15 L/H in fish over 225 mm usually 4.3–4 7, H/S usually 3 8–4 *albus*

16 L/H in fish over 225 mm usually 4 7–4 9, H/S usually 3 9–4 3 *sisco*

17 L/H in fish over 225 mm. usually 5–5 3, H/S usually 4–4 2 *microcephalus*

C^{2} Paired fins long, PV/P usually less than 1 8

D^{1} Maxillary long, H/M usually under 2 9, fins black

18. H/S usually 3 7–4 *manitoulinus*

D^{2} Maxillary shorter, H/M usually over 2 8, fins not always black

E.^{1} Scales usually 70 or more
F^1 Gillrakers usually over 49

19 Gillrakers 49–54, H/M 2 8-3 *tullibee*

20 Gillrakers (48) 52–55 (59), H/M 2 9–3 1 *wagneri*

F^2 Gillrakers usually 47–50, H/M 3–3 2, PV/P usually 1 5–1 7

21 H/E in fish over 250 mm usually more than 4 5 *mendotae*

22 H/E in fish over 250 mm usually less than 4 5 *woodi*

F^3 Gillrakers usually much fewer than 50, PV/P 1 1–1 5

23 Lateral line scales usually 70 or more *magnus*

E^2 Scales usually fewer than 70

24 Gillrakers usually 46–49 *winnipegoesis*

Leucichthys artedi greeleyi, new subspecies

The type is a female specimen, 245 mm long, Cat no 96958 Museum of Zoölogy, collected in Torch Lake, on August 6, 1923, Seventy paratypes were collected at about the same time from various situations in the lake These measure 128–292 mm , 37 are less than 200 mm long Individuals about 150 mm long are usually maturing sexually One fish 128 mm long was found to be maturing

Greeleyi differs from typical *artedi* from Lake Michigan virtually only in the matter of gillrakers, which in the former number (31) 39–43 (46) and in the latter (41) 46–50 (55), and in the matter of relative head length L/H for specimens of *greeleyi* under 212 mm equals (3 7) 3 8–4 1 (4 3), over 212 mm , (4) 4 1–4 4 (4 5) Corresponding values for specimens of *artedi* less than 225 mm and more are (4) 4 2–4 5 (4 6) and (4 1) 4 3–4 5 (5) Pigmentation is in general also reduced The anals and ventrals especially are more often immaculate For a comparison with other races see Tables I–VIII In Tables IX–XIII the various races of *greeleyi* are compared with one another

From August 4 to 7, 1923, gill-nets of 1½-, 2½ and 2¾-inch mesh were lifted from Torch Lake Off Alden in 11 35 fathoms of water 11 specimens were taken on the 4th, on the 5th off Deepwater Point, from 8 to 21 fathoms, 30 were caught, on the

6th, above Lone Tree Point, in 11–16 fathoms, there were 14 fish, on the 7th, east of Torch Lake Village, in 10–20 fathoms, 12 fish, and off the Y M C A Camp in 33–48 fathoms, 4 fish

Torch Lake

Torch Lake lies along the west edge of Antrim County, Michigan, and drains through Round and Elk lakes into Lake Michigan It is about 17½ miles long and varies in width from about ⅝ to 2¼ miles Most of the lake consists of a deep basin, the cross-section of which shows about the same degree of curvature as that of the bowl of a spoon The maximum depth that I found was about 300 feet off Camp Hayo-Went-Ha The depth drops to 275 feet off Clam River and to 250 northeast of Deepwater Point At the south end of the lake the basin constricts into a narrow channel that runs near the west shore to Torch River This central basin appears to be surrounded by terraces like those that hem the lake shores The first is narrow and runs to a depth of about 12 feet The second is overlain by 45–50 feet of water and in at least two localities broadens into an extensive table land off Clam River and between Alden and Torch River bridge The transition to deep water is everywhere abrupt (off Deepwater Point a drop of 125 feet was encountered in the distance of about a rod) The submerged terraces are sandy and are relatively free from rocky stretches or even scattered boulders, and water vegetation is rare The bottom of the deep trough is clay, in many places mixed with marl

Elk Lake

From Elk Lake 184 specimens have been examined, ranging in length from 110 to 312 mm , 107 are less than 200 mm long The smallest specimen, a female, is maturing and so are the next smallest fish at about 130 mm , but about a fourth of the fish under 200 mm are sexually immature and occasionally one of the largest fish shows no indication of spawning in the fall These fish are virtually identical with the Torch Lake race, typical *Leucichthys a greeleyi*

Specimens were taken as follows: on July 29, 1923, off Megazee Point in 7–18 fathoms, 10; on July 30, off the west shore in 16–21 fathoms, 71, and in 7–16 fathoms, 27; on August 3, off Elk River mouth in 6–17 fathoms, 14, and off the Round Lake outlet in 20–27 fathoms, 62. Since the netting used in each set was of approximately the same amount and kind, it seems that conditions are best for the form in the 16–27-fathom depths.

Elk Lake is located in the northwest corner of Antrim County, Michigan, very near the Lake Michigan shore. The connection with Lake Michigan is short, but is now interrupted by a dam, and it is not known whether exchange of fish fauna was possible previous to the construction of this obstacle in 1856. The lake is an elongate body of water, about 9 miles long, rather uniform in its width, which varies from 1¼ to about 1½ miles. Its area is given by Scott, 1921, as 13 square miles.

Except for a 15–20-foot flat about one-half mile wide at the south end and a narrow shelf at the north end, the bottom slopes abruptly, particularly on the east and west shores, to form a central basin of considerable width, which is overlain by depths of 150–190 feet and extends the length of the lake. The bottom along shore to a depth of 5–12 feet is rocky, except along a part of the north shore, where there is sand only, and along part of the south shore, where sand and clay are predominant. Elsewhere the bottom is almost uniformly yellowish clay, mixed with marl, in the deepest water often covered with ooze. Marl is commonest as a constituent of the southern flat. The elevation of the water level on account of the Elk River dam has submerged logs and stumps all along shore, but has not contributed much to the production of shore shoals, so favorable to the usual life of inland lakes. The débris is so widely distributed that it is impossible to pull a seine except in very few areas, and it appears to have served as a protection against wave action, so that accumulations of silt have smothered the bottom over vast stretches. Vegetation is very sparse in any part of the lake, except for small beds of *Potamogeton* in Spencer Bay and in the cove at Elk Lake Inn, and occasional patches of *Chara* in deeper water along the north shore.

Lake Canandaigua

Only three fish, two immature females 113 and 159 mm long, and an adult male 111 mm long, have been examined from Lake Canandaigua They are from the New York Conservation Commission Collection taken in July, 1927 They answer the description of *L a greeleyi*

Canandaigua[2] is one of the Finger Lakes in New York It is regularly elongate, measuring 15 5 by 1 5 miles, with an area of 16 3 square miles Its maximum known depth is 274 feet Drainage is into Lake Ontario through the Seneca River

Keuka Lake

Fourteen adult specimens have been examined from Keuka Lake, 169–191 mm long, and one 232 mm long These are chiefly from the New York Conservation Collection and most of them were taken in July, 1927 The race is much like typical *greeleyi*, and differs only in having very few more gillrakers

Keuka Lake is another of the Finger Lakes It is roughly Y-shaped Dimensions are 19 6 by 2 06 miles, with an area of 18 1 square miles Its maximum known depth is 183 feet Drainage is into Seneca Lake

Owasco Lake

Three adult specimens, 127 180 mm long, have been examined from Owasco Lake, taken in August, 1927, by the New York Conservation Commission Survey The fish are too small to show well the significant characters for separating the races, but until more is known about the Owasco Lake herring the name *greeleyi* may be applied to them The race may be found to have a deeper body and fewer lateral line scales than *greeleyi*

Owasco Lake is a Finger Lake It is regularly elongate, measuring 11 1 by 1 3 miles, with an area of 10 3 square miles Its maximum known depth is 177 feet Drainage is into the Seneca River

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[2] Figures for the Finger Lakes given in this paper are taken from Birge and Juday, 1914*a*

Lake George

Twelve specimens have been examined from Lake George, taken by J R Greeley in September 9, 1929 They range in length from 133 to 173 mm and all are adult They agree in their systematic characters with typical *greeleyi* of comparable size, except that they may have somewhat fewer lateral line scales and the abdominal fins average darker

Lake George is on the boundary between Warren and Washington counties, New York It is about 30 miles long, in few places more than 2 miles wide, and has an area of 50 square miles It drains into Lake Champlain There are three widely separated basins more than 100 feet in depth, and several others that reach 70 feet The deepest water, 187 feet, is in the central basin (Needham, 1922)

Skaneateles Lake

Eight specimens 145–158 mm long and one 241 mm long have been examined from Skaneateles Lake, taken by the New York Conservation Commission Survey in August, 1927 The cisco of this lake was considered by Smith, 1895, to belong, with that of Seneca Lake, to his *L osmeriformis* The fish from the two lakes are very different and Smith's description is clearly not based on a fish of the Skaneateles Lake type, so that this form may not be known as *L osmeriformis* The specimens I have seen are like typical *L a greeleyi*, of similar size, except that the body depth may be greater and the lateral line scales fewer, and the mandible is more often included in the upper jaw The eye in proportion to the head seems to be somewhat smaller also

Skaneateles Lake is a Finger Lake, measuring 15 by 1 46 miles, with an area of 13 9 square miles Its maximum known depth is 297 feet Drainage is through Seneca River into Lake Ontario

Leucichthys artedi huronicus, new subspecies

The type specimen is a female fish, 168 mm long, collected in Rush Lake, Marquette County, Michigan, on September 2, 1924, Cat no 96959, Museum of Zoölogy There were examined eighteen paratypes 138–182 mm long, and one 222 mm long, taken in the summers of 1924 and 1927 from depths of 60 to 240 feet. All but one were adult. Though the lake has been rather extensively netted, only these few fish have been collected. The fish are very like typical *greeleyi*, but have on the average a few more gillrakers, slightly fewer lateral line scales, but principally a shorter snout and maxillary. The color is also darker, and pigmentation is much greater, especially on the paired fins, than is usual even for typical *artedi*.

Comparisons of several important characters of these various races are given in Tables I–XIII. In the last five of these tables all the races of *huronicus* also are compared with one another.

Rush Lake lies in the northwest corner of Marquette County, Michigan, and drains through Pine Lake into Lake Superior. It is elongate in shape, about 1¼ miles long, with a lobe coming off at the southwest end. The maximum width is about ¼ mile. This is the deepest lake known in the region. Most of it is over 60 feet deep and a depth of 270 feet is known.

Chautauqua Lake

I have examined two specimens, 132 and 134 mm. long, taken from Lake Chautauqua, May 18, 1926, from the New York Conservation Commission Collection. It is impossible to assign them positively to any subspecies, but there are indications that the race characters may be like those of *huronicus*. The lateral line scales are rather few in number for this race.

Chautauqua Lake is an elongate lake in Chautauqua County, western New York, about 20 miles long and from ¼ mile to 3 miles wide. Evermann and Goldsborough, 1902, say the greatest depth is reported to be 80 feet, but that the average is no more than twenty. Though it is near the shore of Lake Erie, drainage is south through the Allegheny River.

Lake Desor

Four fish, three 110–118 mm. long and one 161 mm. long, were taken in Lake Desor on September 9–10, 1929, from depths of 5–30 feet. One of the small individuals was found in the stomach of a whitefish. All but the largest are adult. These fish agree with the Rush Lake form in their principal characteristics and are for the present grouped under *huronicus*.

Lake Desor lies in the western half of Isle Royale. It is roughly ovoid, about 3 miles long with a maximum width of half the length. The greatest known depth is 55 feet, much of the lake is at least 35 feet deep. Drainage is through an insignificant stream to Lake Superior.

Leucichthys artedi annensis, new subspecies

The type is a female specimen, 190 mm. long, Cat. no. 96960, Museum of Zoölogy. It was collected in Anne Lake, on August 27, 1924.

From Lake Anne 40 paratypes 182–246 mm. long, all adult, have been examined, 6 of them are over 225 mm. long. Most of the paratypes (27 fish) were taken in a set of a 2½-inch net made on August 27, 1924, in a depth of from 15 to 50 feet. A set on the day previous in the deepest water (78 feet) took only 3 fish. The chief characteristic of the subspecies *annensis* is the low gillraker count, which is on the average higher than that of *greeleyi* and much lower than that of typical *artedi*. It has also a relatively shorter snout than *artedi*, but in other respects this race differs little from it. It has, further, proportionally a slightly shorter head and snout than *greeleyi*. It is like *huronicus*, except that the head is smaller, and like *russeli*, except that the head is smaller and the body depth rather less. For detailed comparison in several important characters with these and other similar races see Tables I–XIII and also XVIII–XXIII.

Lake Anne

Lake Anne lies in the northwest corner of Marquette County, Michigan. It drains into Mountain Lake by a very short stream and thence into Pine Lake and Lake Superior. It is elongate in form, about three quarters of a mile long and less than one quarter wide. It is relatively deep, most of it is 18 feet or more in depth and a sounding of 78 feet is known.

Bernard Lake

Four specimens, 179–194 mm long, in the collection of the Ontario Game and Fisheries Department, taken at Sundridge, Ontario, on August 27, 1929, have few gillrakers and a relatively short head and are, therefore, more like *annensis* than *mackayi*, the commonest form of the area

Bernard Lake is in Strong Township, Parry Sound County It is a regularly elongate body of water with dimensions of about 6 by 2 miles

Leucichthys artedi sargenti, new subspecies

The type is a female specimen, 124 mm long, Cat no 96961, Museum of Zoölogy, taken in Sargent Lake on September 19, 1929 Eight other specimens, taken from Sargent Lake at about the same time, range in size from 56 to 125 mm Two that measure 56 and 60 mm are immature, but the rest, 82 mm long and larger, are adult All were caught in depths of 15–33 feet The race is apparently much dwarfed

It is characterized by relatively few gillrakers, though the average number would probably be slightly higher in larger fish, since in such small fish the shortest gillrakers on the ends of the arches are probably not sufficiently developed to be visible Pigment is present on all the abdominal fins Compared with other races having few gillrakers, it is distinguished from all of them by certain characters It has longer paired fins, a shorter snout and fewer lateral line scales than *musseli* or *greeleyi* It has a deeper body, fewer lateral line scales and longer paired fins than *huronicus*, it is distinguished from *annensis* in the same way and has in addition a longer head, *it differs further from greeleyi* in having a shorter snout (not head) From *atikamek* it differs principally in having fewer gillrakers, and possibly longer paired fins

For details of comparison between these various forms, see Tables I–XIII

Sargent Lake

Sargent Lake is an irregular body of water about 2¾ miles long, with a maximum width of about ¼ mile It lies in the northeastern part of Isle Royale and drains through a feeble stream into Lake Superior. The maximum known depth is 45 feet, much of it is over 25 feet deep.

Lake Richie

Three specimens have been seen from Lake Richie. They measure 42, 90 and 95 mm. in length. All but the first are adult. The two smaller fish were taken from stomachs of pike and hence show no characters other than gillraker number, but the other fish, which was seined on shore on August 18, 1929, is a good specimen. The race is probably like that of Sargent Lake.

Lake Richie is an irregular lake lying in the eastern half of Isle Royale. It is about 2 miles long, but because of a large island in the center of its broadest basin the uninterrupted width is not over ¼ mile. The maximum depth is 39 feet. Much of the lake has at least 25 feet of water.

Siskowit Lake

August 21, 1929, 32 specimens of *Leucichthys* were found on the beach off the outlet of Intermediate Lake. On August 24 one was found floating in the small southeastern arm. These fish are all very small, most of them measuring 40–50 mm. The largest individual is 59 mm. long and is a female with well-developed ovaries, but with no maturing ova.

No specimens of this form were taken in the gillnets set in depths of 50–117 feet, nor in the 1½-inch net floated on the surface over 60 feet of water on August 24, nor were any seined on the beaches after dark. Specimens of *Leucichthys bartletti* were collected in the deep-water sets, both in the netting and in the stomachs of predatory fish.

On account of their being so very small, it is impossible to determine positively the identity of these specimens. They undoubtedly belong to the *artedi* group and may for the present be classed with *sargenti*. Two specimens were counted for lateral line scales and were found to have 68 and 69. Gillrakers number 14 + 28, 14 + 26, 14 + 27, — + 26, — + 26. The fins are long, the body rather deep, and the mandible usually more or less protruding.

Siskowit Lake [3] is the largest lake on Isle Royale. Its greatest length is about 7 miles, an estimate that includes a long narrow bay at the west end; its width is about 1 to 1⅜ miles. On the southeast, by means of a narrow channel (35 ft. wide), is joined another lake, roughly trilobate in form, ¾ mile long and ⅜ mile wide. In the shore-line of the lake there are numerous irregularities that form coves, large and small, principally at the east and west ends, but conditions in most of them are not much different from those of the main lake. There are three large islands (¼–½ mile long) in the eastern half of the lake, one near the center (Ryan), the other two off the south shore. In addition, there are about a dozen smaller ones, some consisting merely of rocks or groups of rocks. The lake discharges into Lake Superior through a small, short stream that rises near the center of the south shore. There are several falls in this stream that probably hinder the ascent of fish from the Great Lake. The stream was discharging when visited.

The vast body of the lake up to the island chain that runs southwest from Ryan Island is over 100 feet deep. The 25-foot contour in most places along the land-bounded sides of this basin runs within 50–100 feet of shore, except that in a few places, chiefly off the north shore, there are narrow flats of shoal water. The largest of those extends off the north-central inlet where a 6-foot shelf runs for over 300 feet. There is a rather extensive plain of about 45 feet to the west of this shoal. Elsewhere the 100-foot contour runs near shore.

The long island chain forms along the bottom a ridge that divides the lake into two main basins. This ridge is broken, so far as is known, only between the northeast peninsula and the rock group to the west. A depth of 68 feet is recorded in the center here (this depth is about equal to that of the floor of the trough along the north shore, but above the level of the plain to the south) with 36–38 feet on either side

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[3] A rather complete description of Lake Siskowit is given because of the peculiar coregonid fauna it contains. Similar hydrographic data are available for the other Isle Royale lakes (Richie, Desor and Sargent) but they are not given here. Descriptions of these lakes will appear at a future date in my report on the ichthyology of the island.

Not much is known about the bottom in deep water In most of the deep sets the bottom material brought up on the anchor stones was fine soft brownish mud common in the basins of the other lakes The set 400 feet west of Teakettle Island brought up a light pinkish-brown clay Along shore the bottom is much as in other lakes where the character of the shore is the same, except that there are less silt and organic ooze over the bottom and the rock fragments have been worn smooth This is due, of course, to the greater opportunity for waves to act on the shores The usual fallen logs are found along shore In the south lake the shores are naturally not so free of silt

Leucichthys artedi hankinsoni, new subspecies

The type is a male specimen, 225 mm long, Cat no 52775, Museum of Zoology, collected by Professor T L Hankinson in Oneida Lake There are also 9 paratypes 211 258 mm long and one 154 mm long All but the last are adult These fish are very different from typical *artedi* and are to be confused only with deep-bodied races They differ from the various races of these, however, in having either fewer gillrakers and lateral line scales, shorter pectorals, maxillary and snout, or greater body depth The abdominal fins in adults are usually rather heavily pigmented, but not black The mandible is as in typical *artedi* The principal systematic characters capable of numerical expression are compared for these and related forms in Tables I–VIII and XIV–XVII

Oneida Lake

Oneida Lake is 11 miles north of Syracuse, New York According to Adams and Hankinson, 1929, it is 21 miles long, with a maximum width of about 5½ miles and an area of 80 square miles, or 51,200 acres Its maximum known depth is 55 feet, over 13 square miles of area are covered by 12 feet of water or less It drains through the Oneida and Oswego rivers into Lake Ontario

Leucichthys artedi birgei (Wagner)

This form was described by Wagner in 1911 The type is a specimen 285 mm long, Cat no 87354, U S National Museum, taken in Green Lake on August 3, 1909 The 36 cotypes of Wagner have been reëxamined to make their data strictly comparable with those for other fish These are now preserved in the Museum of Zoölogy

Birgei differs from typical *L artedi* in having proportionally a somewhat longer head, snout, maxillary and paired fins, a deeper body, smaller eyes, and fewer gillrakers and lateral line scales *Birgei* more often has the mandible shorter than the upper jaw, pigmentation on the abdominal fins is less than in typical *artedi* The ventrals are usually nearly immaculate It is much like *L a greeleyi*, another deep-water lake variety in the matter of long snout and head, but this form has still fewer gillrakers and a much shorter maxillary, and the number of lateral line scales and the mandible are as in typical *artedi* It may be distinguished from any other subspecies of *artedi* by the long snout and maxillary For comparison with other subspecies see Tables I–VIII

The relationship of *birgei* with deep-water types of the Great Lakes has been considered by Wagner, but it approaches closely no known form of these These are known to be variable, but they have not yet been found to be so widely distributed as *L artedi* and hence there are relatively few known variants

Green Lake

Green Lake is in Green Lake County, Wisconsin It is elongate, with maximum dimensions of 7 4 and 2 miles and an area of 11 47 square miles It is by far the deepest of the explored Wisconsin lakes About half the basin's area is covered by 100 or more feet of water and a depth of 237 feet is known The outlet through the Fox River into Lake Michigan is now dammed

Leuchichthys artedi russelli,[4] new subspecies

The type is a female specimen, 217 mm long, collected in Pine Lake, on August 24, 1924, Cat no 96962, Museum of Zoölogy

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[4] Named in honor of Mr John R Russel

From Pine Lake 105 other specimens, paratypes, 127–349 mm long, have been examined, taken during the summers of 1924 and 1927, chiefly from depths of 75 to 100 feet, 52 are under 200 mm long Specimens under 160 mm are usually immature They are much like typical *clemensi* except that they have fewer gillrakers (the range of variation is the same, but the average is different), the body depth is somewhat greater, and the lateral line scales are more numerous From *greeleyi*, *russeli* differs principally in having a deeper body, a somewhat shorter snout, more gillrakers and slightly fewer lateral line scales From *huronicus* it is distinguishable by the longer snout, more numerous gillrakers, greater body depth and reduced pigmentation Furthermore, it is differentiated from *annensis*, the remaining closely similar subspecies, by having a larger head It is compared in detail with this and several other related types in a number of characters in Tables I–XIII and XVIII–XXIII The races of *russeli* are compared with one another in Tables IX–XIII

Pine Lake

Pine Lake is in the northwest corner of Marquette County, Michigan It drains by a short stream into Lake Superior The lake is tripartite and over all is about 2¼ miles long The westernmost part is the largest and by far the deepest It is roundish, with a diameter of a mile Most of its area is over 70 feet deep and several soundings of 120 feet are known The middle part is not known to be over 24 feet deep

Twelve-Mile Lake

Eight adult specimens, 142–178 mm long, have been examined from Twelve-Mile Lake They appear to be like typical *russeli*, but the number of lateral line scales may be found to average low and the paired fins a little long The fish do not average as deep-bodied as *russeli*

This lake, according to the data of the University of Toronto Collection, to which the specimens belong, is in Haliburton County, Ontario

Lake Simcoe

Thirty-two specimens, 142–270 mm long, from the collections of the University of Toronto and the Ontario Game and Fisheries Department, have been examined from Lake Simcoe Individuals under 160 mm are immature They are very like typical *russeli* except that the race appears to have on the average fewer gillrakers and the mandible more often tends to be projecting

Lake Simcoe in the Province of Ontario is about 30 miles long and 18 miles wide, with an area of 280 square miles The southern half has a mean depth of about 50 feet, but greater depths are known Kempenfeldt Bay is said to be over 150 feet deep It drains through Lake Couchiching and River Severn into Georgian Bay (Rawson, 1928)

Leucichthys artedi atikamek, new subspecies

The type is a female specimen, 241 mm long, Cat no 96963, Museum of Zoology, taken in Whitefish Lake Seven paratypes from Whitefish Lake, collected by Professor John Lowe on July 9, 1926, have been examined Four measure 163–170 mm and 3 measure 243–249 mm All appear to be immature These fish differ from other known races of *L artedi* They have fewer gillrakers and lateral line scales, longer paired fins, a shorter snout and maxillary and greater body depth than specimens of typical *artedi* from Lake Michigan The race is different from *clemensi* in having somewhat fewer gillrakers and probably shorter paired fins It is very close to *tullibee*, except that it has many fewer gillrakers and probably shorter paired fins *Winnipegosis* is further differentiated by having fewer lateral line scales, a deeper body, larger head and eyes From *clarensis* it is distinguished principally by having fewer gillrakers and lateral line scales, longer paired fins, smaller eyes and greater body depth Lateral line scales and gillrakers are also fewer *Hankinsoni* is deeper-bodied, has fewer lateral line scales, and shorter snout and maxillary *Albus* has shorter paired fins, a longer snout and shorter head *Russeli* has a few more lateral line scales, shorter pectorals and a much longer snout Body depth is also less In Tables I–XIII *atikamek* is compared with the various related subspecies in certain characters

Whitefish Lake

Whitefish Lake lies just south of Manistique Lake in Mackinac County, Michigan It is irregularly elongate, with a maximum length of about 4½ miles and an area of 6¾ square miles Professor Lowe states that the deepest water is 23 feet

Crawling Stone Lake

Five specimens 151 178 mm long and four 251–306 mm long have been examined from Crawling Stone Lake, taken by the Wisconsin Natural History Survey on September 2, 1909 All but the smallest are adult The race appears to be very close to typical *atikamek* The abdominal fins average paler than in that form

Crawling Stone Lake is in Vilas County, Wisconsin Its form is irregularly elongate, with maximum dimensions of 2 4 and 1 65 miles and an area of 2 5 square miles, or 1600 acres Its greatest known depth is 93 feet It is part of the Chippewa River system

Leucichthys artedi mackayi, new subspecies

The type is a female specimen 183 mm long, Cat no 96064, Museum of Zoology, collected on August 10, 1929, in Stony Lake by the Ontario Game and Fisheries Department Eighteen paratypes, taken at the same time, measure 143–199 mm All are adult

This subspecies is characterized chiefly by the reduced number of gillrakers on the first branchial arch and by the rather greater pigmentation of the abdominal fins Though not often black, these members are usually conspicuously pigmented It differs from *russeli*, which has about the same number of gillrakers, in having a proportionally shorter snout and possibly ventrals The body depth is also less From *clarensis* it differs in having fewer lateral line scales, a longer maxillary, more pigment and possibly longer paired fins

It differs from *huronicus* and *annensis* principally in having more gillrakers, from *artedi* in having fewer gillrakers and lateral line scales, and a longer head and paired fins For a comparison with the various related subspecies see Tables I–VIII All races of *mackayi* are compared in certain important characters with typical *russeli*, *annensis* and *clarensis* in Tables XVIII–XXV

Stony Lake

Stony Lake is in Peterborough County, Ontario I know nothing about any of the lakes in this section and the data labels accompanying the specimens have been copied merely for recording the localities

Pigeon Lake

Twenty-nine specimens from the collection of the Ontario Game and Fisheries Department, collected on August 13, 1929, have been examined from this lake They measure 145–200 mm and are mature The lateral line scales average a little higher than in *mackayi* and the gillrakers seem to be more numerous

Pigeon Lake, according to the specimen label, is in Peterborough and Victoria counties, Ontario

Granite Lake

Eight adult specimens, 120–165 mm long, from the collection of the Ontario Game and Fisheries Department, have been seen from Granite Lake They appear to be very like typical *mackayi*, except that the lateral line scales seem fewer, as in *clemensi*

Granite Lake is in Kenora District, Ontario

Cameron Lake

Seventeen specimens, virtually all adult, 126–156 mm , taken on August 21, 1929, have been examined from the collection of the Ontario Game and Fisheries Department They are very close to typical *mackayi*, except that in the matter of scale number and paired fins they are like *clarensis*

Cameron Lake is in Victoria County, Ontario Trent Valley Canal system

Silver Lake

Four adult specimens, 134–164 mm , taken on November 5, 1927, by the Ontario Game and Fisheries Department may be called *mackayi*

Silver Lake is in Lanark County, Ontario

Sturgeon Lake

Eleven adult fish, 139–175 mm long, taken on August 15, 1929, off McConnell's Island, have been examined from the collection of the Ontario Game and Fisheries Department They agree in their principal characters with typical *mackayi*, except that they have numerous lateral line scales like *clarensis*

Sturgeon Lake is in Victoria County, Ontario

Upper Stony Lake

Eight adult specimens, 120 152 mm long, taken on June 27, 1929, have been examined from the collection of the Ontario Game and Fisheries Department They are like typical *mackayi*, but the females show much larger ova than would be found in any fall-spawning fish

The lake is in Peterborough County, Ontario

Garrison Lake

An adult female, 252 mm long, taken on August 14, 1929, has been seen from the collection of the Ontario Game and Fisheries Department It might be called *mackayi*, except that it has a very short maxillary

The lake is in Arden Township, Frontenac County, Ontario

Kah-She Lake

Two specimens, 174 and 180 mm long, taken on August 6, 1929, have been examined from the collection of the Ontario Game and Fisheries Department They may be called *mackayi*

Kah-She Lake is in Morrison Township, Muskoka County, Ontario

Big Clam Lake

Three fish, 183–195 mm long, taken on September 4, 1929, have been examined from the collection of the Ontario Game and Fisheries Department They have a deeper body and shorter snout and maxillary than typical *mackayi*, but are like them in other respects In the matter of snout and maxillary they are like *clarensis*

Big Clam Lake is in Bethune Township, Parry Sound County, Ontario It is irregularly elongate, a little over 1½ miles long

Sturgeon Lake

Eight adult specimens, 134–183 mm long, in the collection of the Ontario Game and Fisheries Department, taken on August 14, 1929, are most like *mackayi*, though they approach *clarensis* in the matter of lateral line scales

The lake is in Peterborough County, Ontario

Mill Lake

Two specimens, 118 and 177 mm long, in the collection of the Ontario Game and Fisheries Department, taken on August 14, 1929, may be called *mackayi*

The lake is in McDougal Township, Muskoka County, Ontario

Balsam Lake

Four adult fish, 150–158 mm long, taken on August 24, 1929, have been examined from the collection of the Ontario Game and Fisheries Department They may be called *mackayi*, or possibly *annensis*

Balsam Lake is in Victoria County, Ontario

Leucichthys artedi artedi (Le Sueur)

The typical form occurs in all the Great Lakes and in the inland lakes enumerated in the succeeding paragraphs Comparisons with the various related subspecies are given in Tables I–VIII For frequency ratio of the number of gillrakers on the first branchial arch and of lateral line scales for the various races of *L a artedi*, see Tables XXVI–XXVII

Pine Lake

There are 32 specimens from Pine Lake, ranging in length from 203 to 314 mm All are mature There are no differences between these fish and those from Lake Michigan, in fact, it is possible that they are only visitors from the Great Lake (Specimens of

Leucichthys hoyi were found in the lake and these are believed to be immigrants) Between August 9 and 12, 1923, the sets of commercial nets a mile long in the lake, and the experimental nets, all of suitable mesh, took only these few specimens, and it may be that the species leaves the lake in summer One must, however, be very careful in arriving at conclusions on the abundance of fish from the use of gill-nets, for it is well known to fishermen that such apparatus is ineffective under certain conditions

Pine Lake lies in Charlevoix County, Michigan, and is intimately connected with Lake Michigan by a short, deep, navigable channel The main body of the lake is about 13 miles long, varying in width from 1 to 3 miles The "short arm," a narrow body 8½ miles long with a maximum width of a mile, joins the south shore about two thirds of the distance to the outlet The lake is generally deep The published chart shows a maximum depth of 120 feet for the main lake and of 50 feet for the "south arm " Most of the main lake is over 60 feet deep and the shore shelf is very narrow In deep water the bottom was found to be clay mixed with marl

Walloon Lake

Fifteen specimens have been examined, ranging in length from 180 to 209 mm , all of them apparently sexually mature Compared with small specimens of typical *artedi* in respect to the usual characters, it appears that the two forms are much alike, except that the body depth in proportion to its length is apparently a trifle greater in the Walloon Lake fish The snout and maxillary in relation to the head length are slightly shorter, thus approaching *clarensis*

Walloon Lake is located in north-central Charlevoix County It has a length of over 9 miles, a maximum width of about 1½ miles, and an area of about 8½ square miles It drains into Lake Michigan From August 12 to 15, 1923, Dr John Van Oosten and I explored the lake between Eagle Island and its outlet to determine its fish fauna

The lake lies in two distinct troughs of about the same maximum depth, the one forming the main lake and the other, which crosses the main trough, the "north arm" and the deep bay at the lower end In the center of this bay is a rather extensive basin with a depth of 60–80 feet Another large basin equally deep extends from the cove at Wildwood Harbor to near Eagle Island A long flat lying under about 12 feet of water separates the two holes and extends around them, becoming broadest below Eagle Island and off the village of Walloon The transition from this flat to deep water is rather abrupt The flats are marly and are carpeted rather sparsely over most of their extent with *Chara* There are here and there dense patches of *Chara* at depths of 20–25 feet, but the plant disappears beyond 30 feet A few patches of *Potamogeton*, each a few square rods in area, occur in this region

Few small fish were seen along the shores and few were seined Sets of 1½-, 2½- and 2¾-inch linen 60–2 cord gill-nets likewise collected very few fish The nets took the usual species common to the shallow lakes, and, in addition, the lake-herring was found in both basins inside the 40 foot contour

In the northern basin off Wildwood Harbor a 1½-inch net set on August 13 and lifted on the next day from 66 to 70 feet took 2 herring gilled and 75 small perch A 2½- and 1¾-inch net set from 36 to 72 feet took nothing

From the deep hole of the lower basin three sets took herring A 2½-inch net set on August 13, in 66 to 72 feet on very soft black mud and lifted on the next day, took 2 herring ensnarled in its meshes A 1½-inch net at the same depth took 8 herring gilled A 2½-inch net set August 14 and lifted the next day from 66 to 72 feet took nothing, a 1½-inch net from the same depth gilled a herring and a perch The bottom was very soft and black and numerous decaying leaves came up in the nets A 2¾-inch net set off the shore from 12 to 54 feet took 2 herring ensnarled at 40 feet From 40 to 54 feet the net took only one sucker

In nets lifted from 6 to 12 foot off Walloon Village on August 13 only shore-loving species were caught

The herring were not found, therefore, in water shallower than 40 feet, though nets that could gill them were set shallower, but they were taken in 70 feet, the deepest water known in the lake No natives of the area were found to be aware even of the occurrence of this species in the lake, and nothing else is therefore known about its abundance, distribution, spawning season, and so on The specimens collected would not spawn before fall and the spawning season is, then, probably late in the year, as for the same subspecies of *L artedi* elsewhere

Hubbard Lake

There are preserved in the Museum of Zoology 25 small specimens, 147-171 mm long, all sexually mature, and two others, 85 and 143 mm long, that are sexually immature The fish were collected on August 25, 1925, and February 3, 1926 Compared with small specimens of typical *artedi* from Lake Michigan, Hubbard Lake fish differ most in having slightly fewer gillrakers The snout is also a trifle shorter, thus approaching *mackayi* In the matter of L/H, PV/P, AB/V and scale number, the fish are like *artedi*

Hubbard Lake lies in the north-central part of Alcona County, Michigan It is about 7 miles long with a maximum width of about 3 miles Its area is nearly 13¾ square miles It drains through Thunder Bay River into Lake Huron The outlet is now dammed Dr Jan Metzelaar reported a maximum depth of 72 feet

Higgins Lake

Twenty-six specimens have been examined from Higgins Lake, taken in January and August, 1926, 12 of them, 131–138 mm long, are sexually immature, the others, 154 257 mm long, are mature When they are compared with typical *artedi* from Lake Michigan, there is a close agreement in the systematic characters, except that the Higgins Lake fish have somewhat shorter paired fins and rather more numerous lateral line scales The only race with more numerous lateral line scales than typical *artedi* is the Lake Superior one, which Jordan and Evermann, 1911, called *arcturus*

Higgins Lake is in the northwest corner of Roscommon County, Michigan, extending a trifle into Crawford County It is about 7 miles long over all and consists of two ovoid lakes broadly joined, lying nearly at right angles The northern one is largest, measuring 3½ by 4¾ miles and the other 3⅛ by nearly 2 miles The area is about 15½ square miles According to Scott, 1921, the lake is spring-fed with very clear water and its maximum depth is reported to be 125 feet It is at the headwaters of the Muskegon River, which empties into Lake Michigan

Crystal Lake

From Crystal Lake 21 specimens, 181–336 mm long, have been examined All were maturing sexually When they are compared with typical *artedi* from Lake Michigan, it seems that the gillrakers and possibly lateral line scales tend to be slightly fewer in the Crystal Lake fish and the head a trifle larger In other respects they do not differ

Crystal Lake is situated in the western part of Benzie County, Michigan It is about 8 miles long and about 2 miles wide, except on the lower lobe, where the width is about 1½ miles The area is given by Scott as about 16 square miles The same writer states that the maximum depth is said to be as great as 200 feet

Beaver Lake

Two specimens, an immature female 168 mm long and a mature male 193 mm long, have been seen from Beaver Lake Their characteristics seem to be those of typical *artedi* from Lake Michigan, but further analysis may show the race to differ from the typical one

Beaver Lake is located in Alpena County, Michigan, and drains through a series of streams into Thunder Bay of Lake Huron It is roughly elliptical in outline, about 2 miles long, with a maximum width of about ¾ mile According to Dr C L Hubbs, who captured the two herring, the maximum depth is at least 65 feet

Nichols Lake

There are 16 preserved specimens from Nichols Lake, ranging in length from 271 to 320 mm, taken on November 16, 1926 A comparison with typical *L artedi* (specimens over 270 mm long) of those characters that can be numerically expressed shows that the characters of the two forms are much alike, except that the Nichols Lake fish seem to have slightly more lateral line scales and to be deeper-bodied Of 30 Lake Michigan fish over 270 mm in length the L/D value of half falls within the range given above for the Nichols Lake fish and probably a comparison of more, and less carefully selected, specimens from both bodies of water would show a still closer agreement in this character between the two forms It is, therefore, classed as typical form *artedi*

Nichols Lake lies in the northwest corner of Newago County, Michigan It is roughly trefoil-shaped, about three quarters of a mile from the tip of one lobe to that of the other It has no outlet and is spring-fed F H Langlois reports a maximum depth of 57 feet

Portage Lake

There are 34 specimens from Portage Lake Four of them range in length from 164 to 170 mm, the rest, from 255 to 385 mm Specimens in the first group are sexually immature, all those in the second group are mature When they are compared with specimens of similar size from Lake Michigan, it appears that the Portage Lake fish have slightly longer paired fins, especially pectorals, and much greater body depth In the latter character they are about intermediate between *albus* and the largest *artedi* from Lake Michigan (the body depth increases relatively with size)

The form might perhaps be best grouped with *lowei*, since, like this, it seems to represent an approach toward the *tullibee* type

Portage Lake lies on the boundary of Washtenaw and Livingston counties, Michigan It is roughly trilobate, with the central lobe the largest Over all, the length is less than 2 miles The southern lobe is the largest and the widest, being over a mile wide Its maximum depth is reported by Dr C L Hubbs to be about 80 feet The drainage is into Lake Erie through the Huron River

Wolf Lake

The single fish from Wolf Lake is a mature male 126 mm long taken by Dr Metzelaar on November 11, 1927, in 18-30 feet of water It seems to be like typical *artedi* in its characters

Wolf Lake is near the east border of Van Buren County, Almena Township, at the head of the Pawpaw River, a tributary of the St Joseph A depth of 30 feet is recorded by Dr Metzelaar The lake is a small roughly heart-shaped body of water, with a maximum dimension of about 1,000 feet

Coldwater Lake

The single examined fish from Coldwater Lake may be called *artedi* (L/H = 4 3) It is an adult male, 275 mm long, taken on May 27, 1927, in 60–87 feet of water by T H Langlois

Coldwater Lake is in the southern part of Branch County, Michigan It is roughly deltoid in shape, 3 miles long and about 1½ miles wide at the widest part It drains through a network of streams of the St Joseph River system into Lake Michigan Mr Langlois reports a maximum depth of 87 feet

Sandy Bottom Lake

A single specimen, an adult male 280 mm long, taken May 2, 1927, has been seen from Sandy Bottom Lake This fish may be taken for typical *artedi*, though the pectoral is rather long (PV/P = 1 6, L/H = 4 2) The specimen would fit the description of *lowei*

Sandy Bottom Lake is in Green Oak Township, Livingston County, Michigan It drains through the Huron River into Lake Erie It is roundish and about one third of a mile in diameter Dr Metzelaar's reports give a maximum depth of 40 feet

Blind Lake

A single specimen, an adult female 177 mm long, was found dead on the shore on November 5, 1923 The values found for the various systematic characters of this fish fall within the range of those for typical *artedi*

Blind Lake lies in Lyndon Township in the northwest corner of Washtenaw County, Michigan It is a lobe of a larger water system that includes Brewen and Half Moon lakes, which are a part of the Huron River The lobe has a maximum dimension of about 2000 feet There are no data at hand on the depth of this lake

Elkhart Lake

From Elkhart Lake 13 adult specimens 161–188 mm long have been examined, taken by the Wisconsin Natural History Survey on August 18, 1909, in 12–13 m of water These seem to be so close in their characters to small specimens of typical *artedi* from Lake Michigan that the name *artedi* may be applied to them

Elkhart Lake is in Sheboygan County, Wisconsin It has the amoeboid shape so common to many of the Wisconsin lakes Maximum dimensions[5] are given as 1 1 and 0 79 miles and the area as 0 47 square mile The lake is generally deep, about half its area is covered by 35 or more feet of water Its maximum known depth is 113 2 feet

Drainage is though the Sheboygan River into Lake Michigan The outlet is now obstructed

Lac La Belle

An adult female, 142 mm long, taken on August 16, 1911 by the Wisconsin Natural History Survey is the only cisco that has been seen from Lac La Belle It fits the description of typical *artedi*, but the race may be found to belong to one of the forms similar to the typical one

Lac La Belle is in Waukesha County, Wisconsin It is part of the Oconomowoc River system It is irregularly elongate, with maximum dimensions of 2 7 and 1 12 miles and an area of 1 77 square miles The lake is relatively shallow, only about a quarter of its area being over 15 feet deep and only about 12 per cent 35 feet deep Its maximum known depth is 46 6 feet

Little Trout Lake

Little Trout Lake specimens number three and measure 153, 170 and 226 mm All are apparently adult They may pass as typical *artedi*

Little Trout Lake is in Vilas County, Wisconsin It is roughly ovoid, with maximum dimensions of 1 75 and 1 25 miles and an area of 1 5 square miles or 960 acres The greatest known depth is 91 8 feet It belongs to the Chippewa River System

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[5] Figures for Wisconsin lakes given in this paper unless otherwise indicated are taken from Birge and Juday, 1914

Manitowik Lake

M B Trautman picked up two small fish on the beach of Manitowik Lake on August 17, 1928 One of them, 116 mm long, is like *manitoulinus* and the other, 96 mm long, is like typical *artedi*, except that it is like the *manitoulinus* form in respect to its abundant pigmentation The lake is a very large one and there may well be two races of *L artedi* in it Typical *manitoulinus* occurs, so far as is known, in only one of the bays of Lake Huron, and specimens like the one in question, as well as more strongly marked intergrades, are found in the vicinity It is remarkable that the 96-mm specimen is apparently an adult male The other is immature

Manitowik Lake is an elongate body of water in the District of Algoma about 12 miles long and about 1½ miles wide at the widest, draining through the Michipicoten River into Lake Superior

Otisco Lake

Two adult specimens, 244 and 252 mm long, taken by the New York Conservation Commission Survey, have been examined from Lake Otisco They could be matched in any school of typical *artedi* Ciscoes are said to have been absent from the lake originally

Lake Otisco is one of the group of Finger Lakes, about 11 miles southwest of Syracuse, New York, and just east of Lake Skaneateles It is narrowly elongate, measuring 5 4 by 0 76 miles, with an area of 2 9 square miles, maximum depth, 66 feet Drainage is through the Seneca River into Lake Ontario

Cayuga Lake

Two immature fish, 170 and 178 mm long, taken September 10, 1927, by the New York Conservation Commission Survey, are the only representatives of *Leucichthys artedi* that have been seen from Cayuga Lake They may be considered typical *artedi*

Cayuga Lake is the longest of the Finger Lakes in New York State It is like the rest, a blocked valley, measuring 38 1 miles long by 3 5 miles wide and has an area of 66 4 square miles Its greatest known depth is 435 feet Drainage is through the Seneca River into Lake Ontario

Lake Champlain

There are 6 adult specimens from Lake Champlain, 199–266 mm in length The few data indicate that the Lake Champlain fish are very like typical *artedi* from Lake Michigan, but they suggest that more material may show that the population is slightly different from these It may be found in particular that the Champlain form has slightly fewer gillrakers and lateral line scales and slightly longer paired fins It thus approaches *mackayi*

Lake Champlain on the New York–Vermont boundary is also a flooded river valley, 125 miles long and 15 miles wide at the widest, with an area of 595 square miles The greatest depth is 600 feet It drains through Richelieu River to the St Lawrence (Murray, 1910)

Leucichthys artedi osmeriformis (Smith)

Leucichthys osmeriformis Smith was described from Seneca and Skaneateles lakes, but the description, in its critical details at least, was based on a specimen like those from Seneca Lake A very different sort of fish occurs in Skaneateles Lake The type is a specimen bearing Cat no 32162, U S National Museum I have examined from the New York Conservation Commission Collection 12 other specimens from Seneca Lake, all adult, measuring 212–343 mm

The Seneca Lake fish appear to differ slightly from typical *L artedi* in respect to relative size of maxillary and number of gillrakers on the first branchial arch It is compared in these characters with typical *artedi* and other subspecies in Tables I–VIII

Seneca Lake

Seneca Lake is one of the Finger Lakes in New York State It is 35 1 miles long by 3 25 miles wide at the widest and has an area of 67 7 square miles The maximum known depth is 618 feet Drainage is though the Seneca River into Lake Ontario

Leucichthys artedi clarensis, new subspecies

The type is a male specimen, 178 mm long, Cat no 96965, Museum of Zoology, collected in Clear Lake by the Wisconsin Natural History Survey on August 28, 1909 Forty-five paratypes have been examined, taken in summer by the Wisconsin Natural History Survey and Dr Stillman Wright, 39 of them range from 135 to 200 mm in length, the rest, from 227 to 306 mm This form is like typical *L artedi*, except that the lateral line scales average fewer, the snout proportionally much shorter, and the maxillary somewhat shorter The pectoral fins appear to be longer, but these members change in relative size with growth, and when fish of this form and typical *artedi* that are strictly comparable in size are compared, the differences are reduced or disappear The form *clarensis* is like *sisco*, except that the latter has a proportionally shorter head and paired fins, and slightly fewer gillrakers and scales It differs from *albus* mainly in having more lateral line scales, a shorter maxillary and less body depth It is distinguished from most other subspecies of *L artedi* by having either more gillrakers or more lateral line scales and shorter paired fins

A similar race occurs in Allequash, Palette, Silver, Stormy, Muskellunge, Ocauchee, Mamie, Pine, Dead Pike, Fowler and Fence lakes in Wisconsin, and also in Orchard, Whitewood, Ore, Marble, Sand, Round, Douglas and Burt lakes in Michigan The values for H/S, H/M, L/H and PV/P for these races are compared with one another and with typical *artedi* and *sisco* in Tables XXVIII–XXXI See also Table I–VIII and XXIV–XXVII

Clear Lake

Clear Lake is in Oneida County, Wisconsin Its form is amoeboid, with a maximum dimension of 2 1 miles and an area of 1 44 square miles, or 921 6 acres The greatest known depth is 82 feet The map shows no outlet

Allequash Lake

There have been examined from Allequash Lake 24 specimens, ranging in length from 111 to 155 mm , taken in the summers of 1927 and 1928 by Dr Stillman Wright Those less than 130 mm long are sexually immature The specimens are so small that they are comparable only to very undeveloped individuals of larger races, which individuals differ strikingly in some of their characters from their larger brethren The race, however, appears to be very close to *clarensis* in respect to the important characters The abdominal fins average rather paler, but coregonids are generally palest when small

Allequash Lake is in Vilas County, Wisconsin It is rather irregularly elongate, with maximum dimensions of 1 5 miles and 0 88 mile and an area of 0 55 square mile, or 352 acres Its greatest known depth is 24 6 feet, but Professor Juday informs me that about one fifth or one sixth of the area is 20 feet or more in depth Drainage is through Trout Lake to the Chippewa River

Palette Lake

From Palette Lake 28 adult specimens, 167 to 227 mm long, and one immature female, 150 mm long, have been examined They were taken by Dr Stillman Wright in the summers of 1927 and 1928 The race has the short snout and maxillary characteristic of *clarensis*, but the head tends to be relatively small, approaching *sisco*

Palette Lake lies in Arbor Vitae Township, Vilas County, Wisconsin It is named for its resemblance in outline to the artist's implement and, according to a letter from Professor Chancey Juday, dated February 17, 1930, has an area of 203 acres and a maximum depth of 62 feet It lies in the Flambeau system

Silver Lake

From Silver Lake 23 adult specimens, 158–186 mm long, have been examined, and one immature one 134 mm long, taken by Dr Wright in the summers of 1927 and 1928 The form is much like *clarensis*, but seems to approach *sisco* in the matter of head length and in the number of gillrakers

Silver Lake is in Vilas County, Wisconsin It is elongate, with dimensions of 1 mile and 0 2 mile and an area of 0 2 square mile, or 128 acres Its maximum known depth is 55 8 feet Drainage is through the Chippewa system into the Mississippi

Stormy Lake

The collection contains 30 specimens, 159–192 mm long, taken in Stormy Lake by Dr Wright in the summers of 1927 and 1928 Virtually all are adult The race seems to be close to typical *clarensis*

Stormy Lake is in Eagle River Township, Vilas County, Wisconsin It has no outlet, but lies in the Wisconsin River basin It is rather irregular in shape and is about 1½ miles long, Professor Chancey Juday in a letter of February 17, 1930, gives me its area as 493 acres and its maximum known depth as 65 feet

Muskellunge Lake

There have been examined from Muskellunge Lake 42 specimens 145 183 mm in length, virtually all adult, taken by Dr Wright in the summers of 1927 and 1928 The race is much like typical *clarensis*

Muskellunge Lake, formerly called Big Muskellunge, lies in Arbor Vitae Township, Vilas County, very near to Trout, Allequash and Palette lakes It is rather irregular in outline and is about 2 miles long Professor Chancey Juday tells me its area is 927 acres and its maximum depth 65 feet The map shows no outlet, but the lake lies in the Flambeau basin

Lake Ocauchee

Only four adult specimens, 180–226 mm long, taken by the Wisconsin Natural History Survey on September 8, 1909, have been examined from Lake Ocauchee They seem to be very much like *clarensis*, but it may be found that the race is short-headed, like *sisco*

Ocauchee Lake is in Waukesha County, Wisconsin The Oconomowoc River flows through it into the Mississippi Its basin is extremely irregular Maximum dimensions are given as 2 37 and 1 8 miles, with an area of 1 65 square miles, or 1,056 acres The maximum known depth is 94 feet, the average depth is also great, about a third of the lake basin being covered by 50 feet of water

Mamie Lake

There are two specimens from Mamie Lake, taken by the Wisconsin Natural History Survey on August 16, 1907 They measure 199 and 208 mm and both are adult They may pass as *clarensis*

Mamie Lake is in State Line Township, Vilas County, Wisconsin It is elongate, measuring 1 mile by 0 85 mile, with an area of 0 6 square mile, or 384 acres Its maximum known depth is 14 8 feet It drains through the Ontonagon River into Lake Superior

Pine Lake

Eight specimens, 162 192 mm long, taken by the Wisconsin Natural History Survey on August 25, 1911, have been examined from Pine Lake, 2 of them (162 and 167 mm long) are immature They are like *clarensis* in respect to the important characters, but have more lateral line scales and very little body depth The reduction in body depth may, of course, be due to emaciation

Pine Lake is in Waukesha County, Wisconsin, and drains through the Oconomowoc River into the Mississippi, though it is said that there is no surplus water except at flood periods It is elongate, with numerous large and small bays Its maximum dimensions are 2 3 and 1 05 miles, with an area of 1 18 square miles, or 755 7 acres The lake is generally deep, about 40 per cent of its basin being covered by 50 feet of water The greatest known depth is 90 feet

Dead Pike or Genevieve Lake

A single fish, 194 mm long, has been examined from Dead Pike Lake Such a specimen might occur in a school of typical *artedi*, but *clarensis* predominates in the region and until more is known of the characteristics of the race to which it belongs it may be classed under that name

Dead Pike Lake is an irregular body of water about 1¾ miles long, lying in the Flambeau drainage basin in northwestern Vilas County, Wisconsin Professor Chancey Juday informs me that its area is 384 acres and its maximum depth 82 feet The map shows no outlet

Orchard Lake

Three specimens have been examined from Orchard Lake, taken by Dr Metzelaar on May 9, 1927, in 111 feet of water They measure 257–286 mm and are adult They appear to be very like *clarensis*

Orchard Lake is in Oakland County, Michigan It is roundish in outline, with a maximum dimension of about 1¾ miles Dr Metzelaar's notes show a depth of 111 feet Drainage is through the Clinton River

Whitewood Lake

Three specimens have been examined from Whitewood Lake, taken April 12, 1912 They are immature, measuring 213 to 231 mm The fish seem to have the relatively short snout and maxillary characteristic of *clarensis*, but it may be found that the head and pectorals will be longer than is usual for that race

Whitewood Lake, in the southern part of Livingston County, Michigan, is an expansion of the Huron River, three quarters of a mile long over all, with a maximum width of less than one quarter of a mile

Ore Lake

From Ore Lake there are four specimens taken April 26, 1927 Three, 274–327 mm long, are sexually mature, one, 132 mm long, is immature These fish are much like those from Whitewood Lake, except that the depth of body is rather greater, approaching *albus* in this character The large fish are probably very well fed, since the smallest specimen is normal for *clarensis* in this respect

Ore Lake is in the southern part of Livingston County, Michigan It is roundish in form and is about three quarters of a mile in its greatest dimension It maximum depth is reported to be 55 feet The map shows no outlet

Marble Lake

There are two specimens from Marble Lake, 157 and 303 mm long, found dead on August 30, 1927 The smaller one is immature They may be called *clarensis*

Marble Lake is in the eastern part of Branch County and drains through the St Joseph River system into Lake Michigan It measures from end to end about 3 miles The main body of the lake is about ½ mile wide but at the southern end a lobe opens off to the east, increasing the width to 1½ miles There are two narrow lobes at the two corners of the north end A depth of 50 feet is reported by Mr Langlois

First Sand Lake

The single fish from First Sand Lake is an adult female, 278 mm long, taken on September 7, 1927 It may be classed with *clarensis*

First Sand Lake is in Hillsdale County, Michigan It drains through a small creek into the St Joseph River system, which flows into Lake Michigan It is elliptical, being roughly one half mile long and about half as wide It is reported to have a maximum depth of 30 feet

Round Lake

Eight fish have been examined from Round Lake, taken by Professor John Lowe on July 2, 1926 They range in length from 140 to 225 mm , three are mature, 179, 211 and 225 mm long This race appears to be like typical *clarensis*, except that the lateral line scales are fewer It is like *albus*, except that the maxillary averages shorter and the body depth less

Round Lake lies just north of Manistique Lake in Luce County, Michigan It is rounded in outline, with a maximum dimension of over 2 miles It drains through Manistique Lake into the Manistique River Professor Lowe states that a maximum depth of 33 feet was found by him

Douglas Lake

The characters for the Douglas Lake form are based on an examination of 80 fish 137–183 mm long and 4 that are 57–91 mm long Those of the first group are adult and, furthermore, undoubtedly represent the adult population of the lake The collections in Douglas have been made over several years and no fish of greater size have been discovered The fish seem to be nearest to *clarensis*, but differ in having a somewhat longer head, snout, maxillary and paired fins The specimens are very small and in larger fish these parts would undoubtedly be relatively shorter The body depth is, however, a trifle greater than in typical *clarensis* and the lateral line scales fewer, thus approaching *albus*

Douglas Lake lies in the northwest corner of Cheboygan County and drains by a small stream into Burt Lake It is less than 4 miles long and has an area of about 6½ square miles It is roughly trilobate, with the broadest lobe a little less than 2½ miles long There are several depressions in the lake bottom, the greatest one having a depth of 89 feet, according to Welch, 1927

Burt Lake

The 32 specimens from Burt Lake taken by Dr C L Hubbs in August, 1921, are all small, 143–167 mm long These are adult and it is not likely that the species attains much greater size in the lake These fish are much like typical *clarensis*, though the body depth averages possibly a trifle more, and the mandible is usually projecting instead of equal, as in typical *clarensis* The abdominal fins average paler also

Burt Lake is located along the west boundary of Cheboygan County, Michigan It is an elongate body, about 10 miles long The shore-line is interrupted by several peninsulas and promontories, so that the width is greatly variable Its area is 26½ square miles It drains through Mullet Lake, another body of water of similar size, into Lake Huron The maximum depth of the lake is 72 feet Scott, 1921, says much of it is 40–45 feet deep

Fowler Lake

A specimen, 296 mm long, taken on August 17, 1911, by the Wisconsin Natural History Survey in Fowler Lake, may be called *clarensis* It has a very deep body, but typical *clarensis* also is known to be deep-bodied

Fowler Lake is in Waukesha County It receives the waters of the Oconomowoc River which flows through it into Lac La Belle and on to join the Mississippi A 7-foot dam has been constructed across the outlet The lake is irregular in outline Its maximum dimensions are 0 94 and 0 44 mile and its area 0 13 square mile or 83 2 acres There is one deep basin, about a fifth of the lake's area is covered by 35 feet or more of water The maximum known depth is 50 feet

Fence Lake

There are 24 specimens from Fence Lake, all adult, taken by the Wisconsin Natural History Survey on July 23, 1907, and on September 2, 1909 Three measure 237–301 mm , the rest, 166–215 mm These fish are as short-snouted as typical *clarensis*, but the maxillary does not average so short, thus approaching *mackayi* The pectorals are also a trifle long and the head a trifle large One of the largest fish has an L/D value of 3 5, but this value in the other two is 4, and the depth is, therefore, much like that of typical *clarensis* The abdominal fins average somewhat paler also

Fence Lake is in Vilas County, Wisconsin In form it is irregularly ovoid, with maximum dimensions of 3 25 and 2 1 miles and an area of 5 3 square miles or 3392 acres The greatest known depth is 93 feet It belongs to the Chippewa drainage

Leucichthys artedi clemensi, new subspecies

Koelz, 1929, has compared the Lake Nipigon form of herring with typical *L a artedi* and *L a albus* and has shown that it differs from the former principally in having fewer lateral line scales, longer pectoral fins and greater body depth, and from the latter in having fewer lateral line scales, longer pectorals and less body depth Pigmentation is somewhat greater also In the matter of body depth it appears to be intermediate between the two, and in the matter of pectoral length and scale number to be intermediate between these and *L a tullibee* The only other forms with which *clemensi* might be confused are *mackayi*, *russelli* and *clarensis* It differs from the first in having slightly more gill-rakers, somewhat shorter paired fins and more body depth, and from the last in having a longer maxillary and snout and fewer lateral line scales The differences between *russeli* and *clemensi* are stated on page 349 Further studies show that a number of lakes contain herring of this type, and it is here designated as *Leucichthys artedi clemensi*

The type is a male specimen 176 mm long, Cat no 54604, Museum of Zoology, taken August 21, 1923, by Dr W A Clemens There are 83 cotypes measuring 138–253 mm in the same collection For a detailed comparison with other subspecies of *L artedi* see Tables I–VIII, for frequency distribution of the number of gillrakers and of lateral line scales for the various races of *clemensi*, see Tables XXVI–XXVII

Lake Nipigon

Lake Nipigon lies due north of Lake Superior in the province of Ontario It is about 65 miles long by 40 miles wide, but its area is interrupted by numerous islands, so that the total water surface is only about 1,530 miles Throughout most of its area the depth is less than 180 feet, but small areas are known with a depth of about 360 feet It is connected with Lake Superior through the Nipigon River, but a fall probably prevents the interchange of members of the fish fauna

Lake Fanny Hoe

Nine specimens, taken by Professor John Lowe on August 12, 1926, 148–167 mm long, most of them adult, have been examined from Lake Fanny Hoe They are very much like typical *clemensi*, but it may be found that the eyes are relatively somewhat larger and the snout is somewhat shorter

Lake Fanny Hoe lies near the tip of the Keweenaw Peninsula in Keweenaw County, Michigan, very near the shore of Lake Superior It is a little over 2 miles long, with a maximum width of about ½ mile

Mountain Lake

There are 110 specimens from Mountain Lake ranging in length from 143 to 199 mm Virtually all are adult The range of values for all the systematic characters that can be expressed numerically seems to be very like that of typical *clemensi*, except that the number of gillrakers is somewhat lower on the average It is like *russeli* in this respect, but has longer paired fins, slightly smaller head, less body depth and larger eyes

Mountain Lake is located in the northwest corner of Marquette County, Michigan It drains through Pine Lake into Lake Superior It consists of two irregularly elongate lobes, 3 miles long over all, with a maximum width of about ¾ mile Both lobes are relatively deep, much of their basins being covered by over 30 feet of water Depths of 42 feet are known from the small lobe and of 54 feet from the large one

Ives Lake

From Ives Lake 126 specimens have been examined, ranging in length from 122 to 286 mm , 50 of them are under 200 mm in length Specimens less than 160 mm long are usually immature A few maturing fish have been found as small as 141 mm and a few immature fish as large as 170 mm They appear to be very close to typical *clemensi* in their systematic characters, except that the lateral line scales average a trifle higher

Ives Lake is in the northwest corner of Marquette County, Michigan It drains through Pine Lake into Lake Superior, but a high fall prevents accession of fish from the lower lakes It is roughly ovoid and has dimensions of about 1¼ by 1 miles Much of the lake is 50 feet or more in depth and a depth of 102 feet is known

Gulliver Lake

A single specimen, 289 mm long, has been seen from Gulliver Lake Such a fish might occur in a school of typical *artedi* or of *clemensi* and until more is known about the race of herring in Gulliver Lake no name may be finally assigned Determined most by the shortness of the paired fins (PV/P = 1.6, AV/V = 1.4), I provisionally give the name *clemensi*.

Gulliver Lake is in the southwest corner of Schoolcraft County, Michigan, and drains through a creek a mile long into Lake Michigan. It is roughly ovoid, about 1¾ miles long. No data on its depth are at hand.

Trout Lake

The specimens examined from Trout Lake are of varying size: 9 range from 56 to 69 mm., 5 from 139 to 199 mm., and 2 measure 230 and 237 mm. All but those of the first group are adult. They appear to be very similar to typical *clemensi*.

Trout Lake is in Vilas County, Wisconsin, and is part of the Chippewa River system. It is composed of two ovoid parts separated by a short channel, length over all 4.5 miles, maximum width 2.4 miles, area 6.5 square miles, or 4,160 acres. Its greatest known depth is 115 feet.

Leucichthys artedi lowei, new subspecies

The type is a male specimen, 193 mm. long, Cat. no. 96966, Museum of Zoölogy, taken in Hulbert Lake.

The collection contains 70 paratypes 184–231 mm. long, taken by Professor John N. Lowe on July 4, 1926 in 10–15 meters of water. All are adult except 5, of both sexes, 187–218 mm. long. These fish are like typical *artedi* of similar size from Lake Michigan except that they have on the average a few more gillrakers on the first branchial arch, slightly greater body depth, but most particularly, longer pectoral fins. Pigment is more often absent on the anal fin and averages less on the paired fins than in typical *artedi* of similar size. Variation seems to be from typical *artedi* toward *tullibee*.

A comparison of the races *artedi* and *lowei* is given below in respect to the number of gillrakers and length of the pectoral. For comparison with other subspecies see Tables I–VIII and XXVII.

GILLRAKERS ON THE FIRST BRANCHIAL ARCH

SPECIES	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55
L artedi artedi															
Michigan	1	2	7	18	24	46	57	62	49	37	44	22	14	4	
L artedi lowei															
Hulbert						4	3	10	10	20	11	6	6		
Black Oak						1	2	2	11	4	5	2	3	1	

PV/P

SPECIES	1 4	1 5	1 6	1 7	1 8	1 9	2	2 1	2 2	2 3	2 4	2 5
L artedi artedi												
Michigan–225 mm			3	5	20	23	57	21	10	1		
L artedi lowei												
Hulbert		4	14	25	22	6						
Black Oak		1	5	6	13	4	2					

Hulbert Lake is in western Chippewa County, Michigan, apparently in the Lake Superior drainage basin It is roughly ovoid, about 1½ miles long and about ¾ mile wide Professor Lowe says the deepest water found by him is about 89 feet

Black Oak Lake

From Black Oak Lake 31 adult specimens, 148–214 mm long, have been studied, collected on September 16, 1909, by the Wisconsin Natural History Survey They differ from typical *artedi* of similar size from Lake Michigan in having slightly more gillrakers, and more especially in having longer pectoral fins, and hence are much like typical *lowei*

Black Oak Lake is in Vilas County, Wisconsin, almost on the Wisconsin–Michigan boundary It is irregular in form with maximum dimensions of 2 3 and 0 65 miles and an area of 0 73 square miles, or 467 2 acres The maximum known depth is 80 4 feet The map shows no outlet, but it lies in the Lake Superior drainage basin

Leucichthys artedi albus (Le Sueur)

The typical form is from Lake Erie It is known to occur also in Lakes Ontario and Superior It is differentiated from typical *artedi* mainly in having fewer lateral line scales, deeper body and longer paired fins The gillrakers average fewer also None of the fish from the inland lakes have been found to be exactly like the typical *albus*, but specimens from Lake Mindemoya are similar

For comparison with other subspecies of *artedi* see Tables I–VIII and XXVI–XXVII

Lake Mindemoya

From Lake Mindemoya 12 specimens, all adult, 270–304 mm long, have been examined They differ from typical *albus* in having a slightly shorter maxillary and possibly shorter snout and fewer lateral line scales

Lake Mindemoya is on Manitoulin Island in Lake Huron It is about 6 miles long and drains into the Great Lake

Leucichthys artedi sisco (Jordan)

The herring of Tippecanoe Lake, Indiana, was described by Jordan as *Argyrosomus sisco*, but the description is not adequate to distinguish the form from what is now typical *artedi* Jordan and Evermann, 1911, were of the opinion that *L sisco* was not differentiated from the Lake Michigan herring by any technical characters, but made of the latter a subspecies *huronicus*, which has been considered by Koelz, 1929, a synonym of *artedi*

Recent studies show a group of herring from southern inland lakes that differ from typical *L artedi* in having a proportionally shorter head, snout, maxillary and paired fins, being in this respect closest to *L a microcephalus*, which has, however, a still smaller head Since Tippecanoe Lake lies in the region where this small-headed form occurs, I apply the name *sisco* to these fish, having in mind the characteristics of the Corey Lake race as typical, in the absence of an adequate sample from the type locality The two fish at hand from Tippecanoe Lake, immature, 157 and 169 mm long, though not strongly marked examples of the form, at least fit into the range of variation, and it is possible that further material from the type locality will show the race to be differentiated from typical *artedi* like the Corey Lake fish

If the race is not different from *artedi*, or is different from the Corey Lake form, then another name may possibly be applicable, *bisselli*, which Bollman, 1890, applied to the *L artedi* of Rawson and Howard lakes of Kalamazoo County, Michigan I myself have not seen these fish[6]

A comparison of the race *sisco* with typical *artedi* and *microcephalus* is given in Tables XXXII–XXXVII See also Tables I–VIII, XXVII and XXX–XXXI

Corey Lake

From Corey Lake 25 adult specimens have been examined, ranging in length from 260 to 312 mm They were taken in 33–45 feet of water on June 16, 1927, by T H Langlois These fish are almost identical in their systematic characters with those of Gogebic Lake (typical *microcephalus*), except that the body has less depth on the average, the lateral line scales are fewer, and the head is larger The head is, however, proportionally much smaller than in specimens of Lake Michigan *artedi* of the same size It differs, then, from typical *artedi* principally in having a proportionally shorter head, snout, maxillary and paired fins It has also slightly fewer gillrakers and lateral line scales It is much like *clarensis* in respect to relative length of snout and maxillary, but has a shorter head than this form

Corey Lake is near the west border of St Joseph County, Michigan It is roughly triangular and measures about 1¼ miles from tip to tip T H Langlois reports the maximum depth to be 45 feet It drains into Kaiser Lake, which has no outlet, according to Scott

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[6] A specimen 213 mm long supposed to come from Kalamazoo County is certainly not like the Corey Lake form It has a value for I /H of 4 2, for PV/V of 1 5

Klinger Lake

Six specimens have been examined from Klinger Lake They measure 306–376 mm and are all adult They were taken on June 15, 1927, in 40–58 feet of water, by T H Langlois The snout and maxillary average short, but the head, considering the great size of the specimens, is rather long The pectoral fins are decidedly long The form thus approaches *clarensis*, but pending accumulation of further data, it is grouped here The anal and ventral fins are usually immaculate, so that the form is paler than most races of *L artedi* The number of lateral line scales appear high enough for *arcturus*

Klinger Lake is near the south border of St Joseph County, Michigan It drains into Lake Michigan through a tributary of the St Joseph River It is roughly ovoid, with a maximum dimension of about 1¾ miles Mr Langlois reports that most of the lake is 18 feet or more in depth and about one fourth of its area is covered by 40–85 feet of water

Murry Lake or Nagel Lake

A single adult fish from Murry Lake, 200 mm long, apparently belongs to this race

Murry Lake lies between Vergennes and Grattan townships along the east border of Kent County, Michigan In shape it is an irregular loop coiled back on itself so that the ends are separated by only a few rods of land The formation measures 1½ by about ¾ miles It is part of the Grand River system, which flows into Lake Michigan No data are at hand on the depth of this body of water

Harwood Lake

There are 5 adult specimens from Harwood Lake, measuring 242–256 mm, taken by Oscar Romig on December 7, 1925 The fish have a relatively short snout and maxillary and few gillrakers, being thus differentiated from typical *artedi* The head seems to be proportionally short, and pending the accumulation of more data the race is called *sisco*

Harwood Lake lies on the east border of Cass County, Michigan It is a little over one half mile long with a maximum width of less than one quarter of a mile It is part of the St Joseph River system There are no data at hand on the depth of the lake

Oconomowoc Lake

From Oconomowoc Lake 10 adult specimens, 235–272 mm long, have been examined These are from the collection of the Wisconsin Natural History Survey and were collected on March 15, 1915 The characters of these fish are very close to those of *sisco*, except that it seems that the number of gillrakers is high

Oconomowoc Lake is in Waukesha County, Wisconsin It consists of two roughly ovoid basins separated by a shallow strait The main basin measures 0 75 by 0 85 mile, with an area of 0 99 square mile, or 633 6 acres, and the northeast basin measures 0 75 by 0 15 mile, with an area of 0 28 square mile, or 179 2 acres Both basins are deep and about half of the lake is covered by more than 30 feet of water The lake's maximum known depth is 62 6 feet, in the main basin The Oconomowoc River flows through the lake into the Mississippi

Island Lake

Only 4 specimens, 180–200 mm long, have been examined from Island Lake They are from the Wisconsin Natural History Collection and were taken on September 12, 1928 These fish have relatively small snouts, maxillaries and heads and are thus to be grouped with the race *sisco*

Island Lake lies in Bayfield County, Wisconsin, in the Lake Superior drainage area It is irregular in form with a length of 2 miles Its maximum known depth is 55 feet, according to Professor George Wagner's notes

Lake Geneva

The occurrence of a cisco in Lake Geneva has long been known and the fish has been several times referred to in literature as *Leucichthys sisco* (Jordan) Jordan, 1911, says in writing of *L sisco* of Lake Tippecanoe, the type locality, that it is "merely a landlocked form of the ordinary Lake Michigan herring, smaller, softer in flesh, and more plump, but showing no technical differences whatever" A study of 115 specimens, 156–235 mm long, all adult, shows that the Geneva Lake fish differ from typical *artedi* in having on the average slightly shorter paired fins, head, snout and maxillary and possibly fewer gillrakers, and the name *sisco* is therefore retained for them

Lake Geneva is in Walworth County, Wisconsin It is irregularly elongate, with maximum dimensions of 7 5 and 2 miles and an area of 8 76 square miles About 60 per cent of the lake is 50 or more feet deep and a depth of 142 feet is known It is mainly spring-fed The drainage is through the Fox River into Lake Michigan The outlet is now dammed

Gordy Lake

Four adult specimens, 301–325 mm long, have been examined from Gordy Lake, from the collection of Professor Will Scott of the University of Indiana Only in the matter of the H/M and L/H values do they appear to be differentiated from typical *artedi* In respect to relative head length they are like *sisco*, and pending the acquisition of more data the race is called *sisco*

According to the specimen label, Gordy Lake is in Noble County, Indiana, about 5 miles southeast of Cromwell, and is over 11 meters deep

Indian Village Lake

Three specimens have been seen from Indian Village Lake from the collection of Professor Will Scott They measure 282, 304 and 337 mm and are adult They seem to fit *artedi* very closely except that they have relatively short maxillaries, and their only claim to being grouped with *sisco* rests on geographical grounds

According to the specimen label, Indian Village Lake is in Noble County, Indiana, in the same chain of lakes as Gordy, with two small shallow lakes intervening, and is 6 meters deep

Lake James

A specimen, adult, 208 mm long, U S National Museum no 64700, has been seen from Lake James It might well be from

Lake Michigan, so far as its characteristics are concerned, but since it comes from Indiana, near the type locality of *sisco*, it is tentatively grouped under that rubric

James Lake is in Steuben County, Indiana It drains through the St Joseph River into Lake Michigan

Lake Tippecanoe

Lake Tippecanoe is in Kosciusko County, Indiana, and drains through the Tippecanoe River to the Wabash Its area is given by Large, 1897, as 1 41 square miles, and its maximum depth as 121 feet Much of it is over 35 feet deep

Leucichthys artedi microcephalus, new subspecies

The type is a male specimen, 272 mm in length, Cat no 96967, Museum of Zoology, taken in Gogebic Lake in the summer of 1929 by Dr Jan Metzelaar

Nine adult paratypes, 213–314 mm long, taken at the same time, have also been examined from Gogebic Lake These fish differ from any known race of *L artedi* in having very short heads and very short paired fins They have, in addition, a somewhat deeper body, slightly fewer gillrakers, shorter snout and maxillary and more heavily pigmented abdominal fins than specimens of typical *artedi* The race is compared for most of these characters with typical *artedi* and with *sisco* in Tables XXXII–XXXVII See also Tables I–VIII

Gogebic Lake

Gogebic Lake lies in the two counties of Ontonagon and Gogebic in the state of Michigan (Upper Peninsula) It is about 13 miles long, with a maximum width of 2½ miles and an average width of about 1½ miles The area is over 20 square miles Over most of the lake, according to the notes of the late Dr Jan Metzelaar and the report of Mr Gerald McCrimmon, who worked with Dr Metzelaar on the lake, the water depth is 18 20 feet A small area covered by a maximum depth of 33 feet lies to the northward of Alligator Point The lake drains through the Ontonagon River into Lake Superior

Leucichthys artedi manitoulinus (Jordan & Evermann)

The type is Cat no 64670, U S National Museum The form is differentiated from typical *artedi* by its deeper body, longer paired fins, head, and maxillary, larger eyes and fewer gillrakers and lateral line scales It differs from all other deep-bodied races in having a longer maxillary, except *birgei* From this it may be distinguished principally by having a shorter snout and much darker fins It is compared with the various subspecies of *L artedi* in Tables I VIII and XIV-XVII

Manitowik Lake

An immature fish, 116 mm long, picked up dead on the beach of Manitowik Lake, by M B Trautman on August 17, 1928, is apparently a representative of the form *L a manitoulinus* Another specimen so found is described on page 338 as closest to typical *artedi*

Leucichthys artedi tullibee (Richardson)

Six specimens have been seen from Pine Island Lake, Saskatchewan, the type locality of *Coregonus tullibee* of Richardson These specimens were loaned by Mr J R Dymond of the University of Toronto and were described by him in 1928 The name *tullibee* has been generally used in literature for any deep-bodied *Leucichthys* The specimens range in length from 297 to 355 mm, and were collected in the winter of 1926–27 Their principal systematic characters are shown in Tables I–VIII and XIV–XVII, where they are compared in detail with other subspecies of *L artedi* and with other races of *tullibee* The abdominal fins are decidedly pigmented, much more than is usual for typical *artedi*, but are not black

Pine Island Lake

Pine Island or Cumberland Lake is in northern Saskatchewan and drains through the Saskatchewan River It is very irregular in outline and measures about 45 miles over all

Lake Winnipeg

Fourteen specimens, 217 to 293 mm long, have been seen from Lake Winnipeg, they were collected from fish dealers in Grand Haven, Michigan They are much like typical *tullibee*, but have greater body depth and fewer lateral line scales

Lake Winnipeg in the province of Manitoba is about 250 miles long by 60 miles wide and has an area of 9,000 square miles The maximum depth is 90 feet It receives the Saskatchewan River and the drainage from Lakes Winnipegosis and Manitoba, the Winnipeg River and the Red River and drains by the Nelson River through several small lakes into Hudson Bay (Murray, 1910)

Lake of the Woods

From Lake of the Woods eight individuals 47-130 mm long and two 204 and 232 mm long have been examined Only the two largest fish are adult If allowance is made for their small size, they appear to be very close to typical *tullibee*

Lake of the Woods, which is on the Ontario-Minnesota boundary, is about 70 by 60 miles, with a water area of 1,500 square miles The outline is much indented and the north portion is filled with islands Its main tributary is the Rainy River, which drains from Rainy Lake, and its outflow is Winnipeg River to Lake Winnipeg (Murray, 1910)

Rainy Lake

A single adult specimen, 273 mm long, has been seen from Rainy Lake, no 64677, U S National Museum Collection It may be called *tullibee*

Rainy Lake on the Minnesota–Ontario boundary is a body of water of very irregular outline, measuring over all about 50 miles Drainage is into Lake of the Woods

Lake Wakesiu

Three specimens, 227, 327 and 367 mm long, from the University of Toronto Collection, taken in Lake Wakesiu during the summer of 1928, are apparently like typical *tullibee*, but they may be found to have more numerous lateral line scales The smallest fish is immature

Lake Wakesiu is about 50 miles north-northwest of Prince Albert, Saskatchewan It is about 16 miles long

Leucichthys artedi wagneri, new subspecies

The cisco from Tomahawk Lake is sufficiently different from any known cisco to merit a name The type is a female specimen, 214 mm long, Cat no 96968, Museum of Zoology Eight paratypes have been examined, taken on August 25 and 26, 1909, by the Wisconsin Natural History Survey They measure 183 224 mm and are all adult The most striking characteristic of the race is the high number of gillrakers, it is equaled in this respect only by *Leucichthys hubbsi* and exceeded only by *L nipigon* A comparison follows with both these species and typical *L artedi* in those characters capable of numerical expression

GILLRAKERS ON THE FIRST BRANCHIAL ARCH

wagneri (48) 52–55 (59) [7]
hubbsi (47) 51 54 (57) [8]
nipigon (54) 56–59 (66) [9]
artedi (41) 46–50 (55) [10]

LATERAL LINE SCALES

wagneri 68–75
hubbsi (63) 67–75 (79) [7]
nipigon (68) 72–77 (82)
artedi (68) 77–87 (94)

L/H

wagneri 4 4 2
hubbsi (3 5) 3 7–4 (4 2)
nipigon (3 8) 3 9 -4 (4 1)
artedi (4) 4 2–4 5 (4 6)

H/E

wagneri 3 8–4 (4 2)
hubbsi (3 5) 3 8–4 (4 3)
nipigon (3 8) 4 2–4 4 (4 5)
artedi (3 5) 3 7–4 (4 3)

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[7] These and succeeding figures for *wagneri* are based on an examination of 9 specimens 183–224 mm long

[8] These and succeeding figures for *hubbsi* are based on an examination of 97 specimens 136–213 mm long

[9] Figures for *nipigon* so marked are based on an examination of 43 specimens 220-447 mm long All others are based on 16 specimens less than 300 mm long

[10] Figures for *artedi* so marked are based on an examination of 391 specimens 127–367 mm All others are for 146 of the specimens less than 225 mm long

H/S

wagneri 3.9–4.3(4.5)
hubbsi (3.4)3.7–3.9(4.3)
nipigon (3.5)3.7–3.8(4)
artedi (3.4)3.6–3.9(4.1)

H/M

wagneri (2.7)2.9–3.1
hubbsi (2.4)2.6–2.8(3)
nipigon 2.5–2.8
artedi (2.4)2.7–3(3.1)

PV/P

wagneri (1.4)1.5–1.7
hubbsi (1.2)1.3–1.5(1.8)
nipigon (1.4)1.5–1.6(1.8)
artedi (1.6)1.8–2.1(2.5)

AV/V

wagneri (1.3)1.5(1.6)
hubbsi (1.1)1.3–1.5
nipigon (1.2)1.4–1.5(1.6)
artedi (1.3)1.5–1.7(2)

L/D

wagneri 3.5–3.7(3.9)
hubbsi (3.5)3.8–4.2(5.1)
nipigon (3.5)3.8–4(4.1)
artedi (4.1)4.4–5(5.8)

Thus it is seen that, compared with *L. hubbsi*, *wagneri* has a proportionally shorter head, snout, maxillary, and paired fins and less body depth. Compared with *L. nipigon* it has fewer gillrakers, a proportionally shorter head, snout and maxillary and greater body depth.

It differs from *L. artedi* chiefly in having many more gillrakers, fewer lateral line scales, a proportionally longer head and paired fins, a shorter snout and greater body depth. In all these characters, except in the number of gillrakers, *wagneri* is close to the *tullibee* form of *L. artedi*. It is compared in detail with the subspecies of *L. artedi* in Tables I–VIII.

Wagneri is regarded as a subspecies of *L. artedi*. The arguments in favor of this consider the fact that *L. artedi* is the generally distributed species in the inland lakes and in waters where other species of *Leucichthys* have been described *L. artedi* has been present also, and further, that in its external features, such as shape of the body, of the head, and so forth, it is much like this species. (It is almost identical with a known subspecies of that form, differing only in having more gillrakers than any other known race, although there are such that vary from the typical form in the opposite direction.) On the other hand, it might be said that the form in question is a modified race of *L. nipigon* or *L. hubbsi*, and the only possible reply would be that *L. nipigon* is not known to occur south of Lake Nipigon. *L. hubbsi* is probably a derivative of some Great Lakes *Leucichthys* (possibly *kiyi* or *nigripinnis*, or even *nipigon*) and *L a wagneri* might be derived from the same stock

Tomahawk Lake

Tomahawk Lake is in Oneida County, Wisconsin It is very dissected in outline, with a maximum length of 4 5 miles and an area of 5 7 square miles, or 3,648 acres Its greatest known depth is 73 8 feet A dam at the outlet of Kawaugesaga Lake has intimately joined Tomahawk with the Minocqua-Kawaugesaga Lake Drainage is through the Wisconsin system into the Mississippi

Leucichthys artedi mendotae, new subspecies

The type is a male specimen, 252 mm long, Cat no 96969, Museum of Zoölogy, taken by the Wisconsin Natural History Survey on August 18, 1914 Paratypes numbering 17, taken the same year, measure from 220 to 321 mm This form differs from *tullibee* in having on the average a relatively shorter maxillary, somewhat less body depth, shorter and paler paired fins, and smaller head and eyes It differs further from *winnipegonsis* in having more gillrakers and lateral line scales It differs from *woodi* in having a relatively much smaller eyes These and other characters are compared for the various subspecies of *L artedi* in Tables I–VIII and XIV–XVII

Mendota Lake

Mendota Lake is in Dane County, Wisconsin, and is a part of the Mississippi drainage system It has rather regular shore-lines and measures 5 9 and 4 6 miles on the lines of greatest dimensions Its area is 15 2 square miles, or 9,728 acres The maximum known depth is 84 feet The average depth is also great and over half of the basin is covered by 50 feet of water

Hammills Lake

There is one specimen, 326 mm long, from Hammills Lake, collected by the Wisconsin Natural History Survey on September 2, 1908 It may be called *mendotae* (the H/E value is 4 7)

Hammills Lake is in southwestern Bayfield County, Wisconsin

It is roughly heart-shaped with maximum dimensions of 1 by 0 55 mile Its area is 0 35 square miles, or 224 acres It lies in the drainage area of the St Croix River, a tributary of the Mississippi The greatest known depth is 49 2 feet

Leucichthys artedi woodi, new subspecies

The type is a male specimen, 250 mm long, Cat no 96970, Museum of Zoölogy, collected by the Wisconsin Natural History Survey on August 27, 1907, in North Twin Lake Paratypes, 14 in number, 12 measuring 228 to 256 mm and 2 measuring 154 and 190 mm have been examined All but the two smallest are adult The form is very like *winnipegosis*, but may be separated from it by the more numerous lateral line scales and reduced body depth It is like *mendotae*, except that it has relatively much larger eyes It differs from *tullibee* in having slightly fewer gillrakers, a shorter maxillary and probably shorter and paler paired fins Comparison of several important characters with these and other subspecies is given in Tables I–VIII and XIV–XVII Pigmentation is about as in typical *artedi*

North Twin Lake

North Twin Lake is in northeastern Vilas County, Wisconsin, near the Michigan–Wisconsin boundary It is rather regularly elongate in form with maximum dimensions of 3 2 and 0 75 miles and an area of 1 7 square miles, or 1,088 acres It drains through the Wisconsin River into the Mississippi Its maximum known depth is 88 6 feet

Minocqua-Kawaguesaga Lake

There are 29 adult specimens, 242–338 mm long, taken from this lake by the Wisconsin Natural History Survey, mainly in September, 1906 Several of them have a very high number of gillrakers and fit exactly the description of *wagneri*, but the majority have a rather low gillraker count (see Table XIV) and for this reason the form is grouped with *woodi* The fish with numerous gillrakers apparently differ from the others in no other structural features. It is possible that they are migrants from Tomahawk Lake.

Minocqua Lake is in the northeastern part of Oneida County, Wisconsin. It is now intimately connected with Kawaguesaga Lake as a result of a dam across the outlet of the latter, and the chain is known as Kawaguesaga Lake. The raising of the water-level has also resulted in the establishing of a broad deep thoroughfare between this lake and Tomahawk Lake. The dam was built in 1890, but there was between Minocqua and Tomahawk lakes "a stream large enough for fish to pass through before the dam was built" (according to a letter from Professor Chancey Juday, dated February 17, 1930).

The lake is very irregular. Its maximum dimension is 4.25 miles with an area of 3.23 square miles, or 2,067.2 acres. The greatest known depth is 55.8 feet. It drains through the Wisconsin River system into the Mississippi.

Long Lake

Nine specimens have been examined from Long Lake, taken by the Wisconsin Natural History Survey on August 29, 1907. They measure 183–210 mm. and all are adult. The race appears to be *woodi*.

Long Lake is in Hackley Township, Vilas County, Wisconsin, at the headwaters of the Wisconsin River. In form the lake is rather regularly elongate. It measures 1.4 by 0.6 miles and has an area of 0.7 square mile, or 448 acres. Its greatest known depth is 55.8 feet.

Shell Lake

A single fish, 355 mm. long, has been seen from Shell Lake. It may temporarily be called *woodi*.

Shell Lake is in the southern part of Washburn County, Wisconsin. It is roughly palette-shaped, with a maximum length of 3¼ miles and a maximum width of 2½ miles. The area is 5 square miles, or 3,200 acres. It drains through a network of bodies of water into the St. Croix River, a tributary of the Mississippi. Its maximum known depth is 49½ feet.

Wolf Lake

Two adult fish, 277 and 290 mm. long, collected in Wolf Lake on April 25, 1922, seem to be like *woodi*, except that the fins are darker in color. It is assumed that this is due to environmental conditions and partly for that reason, partly because it is not easy to draw the line between a dark-colored fish and one of usual color, the form is not separated. It will probably be found to have much longer paired fins than the typical race.

Wolf Lake is in Beltrami County, Minnesota, it drains into the Mississippi.

Charter Lake

Two adult specimens, 278 and 292 mm. long, collected by Mr. J. R. Dymond in Charter Lake, seem to be much like the Wolf Lake form mentioned in the previous paragraph and are also called *woodi*.

Charter Lake, according to the label accompanying the specimens, is near Parry Sound, Ontario.

Whitestone Lake

Two specimens, 169 and 170 mm. long, in the collection of the Ontario Game and Fisheries Department, taken on August 17, 1929. These may be placed with *woodi*, though the body depth is less.

Whitestone Lake is an extremely irregular body of water in Hagerman Township, Parry Sound County, Ontario. It is 2¾ miles long over all with a maximum width of about ¾ mile. Drainage is into Georgian Bay.

Cass Lake

Two very small specimens, 49 and 53 mm. long, found dead in the summer of 1921, are provisionally called *woodi*. They certainly are deep-bodied, with lateral line scales numbering about 71 in each.

Cass Lake is in northern Minnesota, in the headwaters of the Mississippi.

Leucichthys artedi magnus, new subspecies

The type is a male specimen, 382 mm long, Cat no 96977, Museum of Zoölogy, taken in Lesser Slave Lake at Fort Smith, Alberta, in the winter of 1921–22, by collectors for the University of Toronto Four other specimens, paratypes, 295–397 mm long, have been examined from Lesser Slave Lake, they are in the University of Toronto Collection

These fish are large, but they are by no means maximum examples of the genus *Leucichthys* They are similar to *winnipegosis*, so far as can be ascertained from the comparison of two so strongly contrasted size-groups, but it will probably be found that the lateral line scales average higher in number, and the paired fins longer and much darker in color For a comparison with other similar subspecies see Tables I–VIII and XIV–XVII

Lesser Slave Lake

Lesser Slave Lake in northern Alberta is 60 miles long with an average breadth of 8 miles and an area of 480 square miles It drains by the Lesser Slave River into Athabasca River Most of it is less than 10 feet deep (Murray, 1910)

Leucichthys artedi winnipegosis, new subspecies

The type is a female specimen, 191 mm long, Cat no 96971, Museum of Zoölogy, taken off Whiskey Jack Island in January, 1922 There are also 8 paratypes, 188–204 mm long, 3 of them in the University of Toronto Collection The form is much like *tullibee*, but differs from it in having many fewer gillrakers and fewer lateral line scales The body probably averages deeper also A comparison with the forms of *L artedi* in several important characters is given in Tables I–VIII and XIV–XVII Pigmentation is about as in typical *artedi*

Lake Winnipegosis

Lake Winnipegosis is about 130 miles long by 20 miles wide and has an area of 2080 square miles The maximum depth is 38 feet

Outlet is through the Waterhen River to Waterhen Lake to Lake Manitoba (Murray, 1910)

Lake Wabigoon

Five adult specimens, 266–325 mm long, have been examined from Lake Wabigoon, mainly from the University of Toronto Collection They appear to be very close to typical *winnipegosis*

Lake Wabigoon is a large irregular lake in Kenora District, Ontario, about 20 miles long Drainage is into Lake Winnipeg

Otter Lake

Five adult specimens, 167–183 mm long, have been seen from Otter Lake, taken by Professor Lowe on September 12, 1925 They are much like *winnipegosis*, except that the head is relatively smaller The snout may be found to average larger also

Otter Lake is in the eastern part of Houghton County, Michigan (Upper Peninsula), near the shore of Lake Superior It drains through Sturgeon River into Portage Lake The lake's shape is roughly elliptical with two elongate bays at each end, about 3 miles long with a maximum width of less than a mile Professor Lowe says the greatest depth is 30 feet

Lake Van Etten

A single immature fish, 128 mm long, has been seen from below the dam at the outlet of Van Etten Lake Apparently it may be classified as *winnipegosis*

Van Etten Lake is a lake about 3½ miles long in northeastern Iosco County, Michigan, lying hard against the Lake Huron shore It is in the main 15-25 feet deep, according to the notes of Dr Metzelaar Drainage is by a small stream through a small lake (one half mile long) into the Au Sable River

Portage Lake

A single specimen has been seen from Portage Lake, taken by T Vergeer on August 12, 1927 It is an adult and measures 210 mm Several specimens of *Leucichthys* supposed to be from Portage Lake, seized by game protectors, are in the collections of the Museum of Zoölogy, but they are of species not occurring in the Great Lakes area and very probably were caught in the lakes of the Prairie Provinces The Portage Lake fish may be called *winnipegosis*

Portage Lake is a large inland bay of Lake Superior in Houghton County, Michigan (Upper Peninsula) A ship channel now affords passage through the lake from one side of the Keweenaw Peninsula to the other The main body of the lake is some 6 miles long and about 2 miles wide, three long narrow arms extend out for several miles each

Kenogami Lake

An adult male in the collection of the Ontario Game and Fisheries Department, taken on October 12, 1925, may be called *winnipegosis* It has, however, a value for L/D of 3 9, and the paired fins are much darker

Kenogami Lake is in the Temiskaming District, Ontario

Leucichthys bartletti, new species [11]

(Pl XXXIX)

The type is a female specimen, 158 mm long, Cat no 96976, Museum of Zoölogy, taken off Teakettle Island in Siskowit Lake, Isle Royale, Michigan on August 21, 1929, in 100 feet of water Twelve paratypes were collected in about the same place as follows 4 on August 23, in 112–117 feet of water, 8 on August 25, in 50–110 feet, 2 of them from the stomachs of trout and lawyers, together with other specimens of *Leucichthys* too digested to identify The species apparently shares its habitat with the lake trout, whitefish and lawyer The lawyer regularly swallowed the specimens of *Leucichthys* entangled in the nets, sometimes releasing them only at the surface, so that virtually all the paratypes are semidigested

The body form is in general like that of *L zenithicus* The predorsal contour is not humped at the nape The head is long and of little depth and is contained 3 6 (3 6–3 9) times in the

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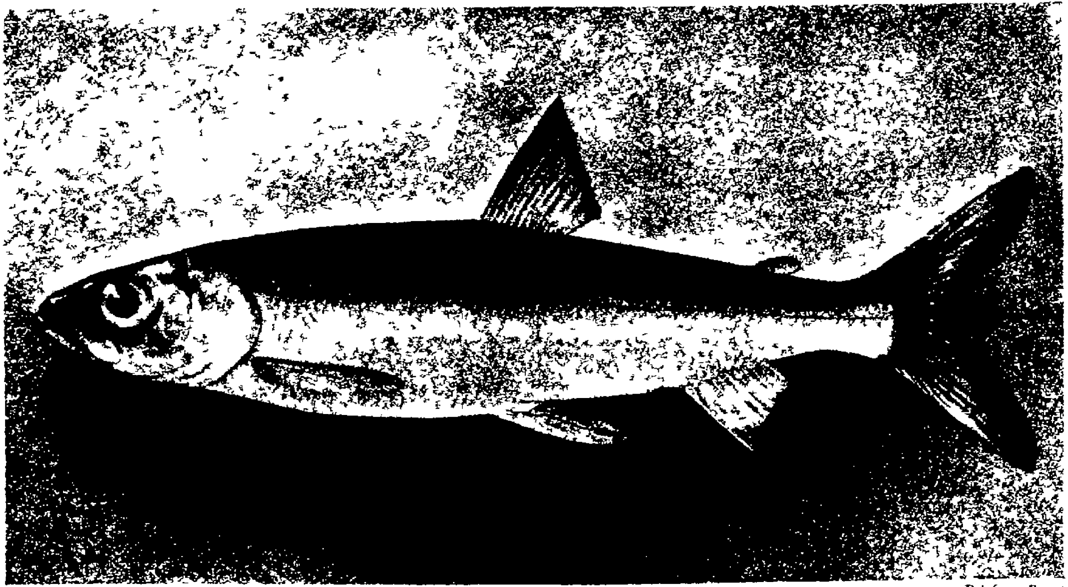
[11] Named in honor of Professor H H Bartlett

XXXIX



(Del Grace Eager)

Leucichthys bartletti n sp

total length H/E equals 3 6[3 3-3 8(4)], H/S 3 5(3 3-3 6), H/M 2 2(2 2-2 5), PV/P 1 5[1 5,1 6(1 8)], AV/V 1 2(1 2-1 5), L/D 4 7(4 7-5 4), gillrakers 13 + 21 (34-37), lateral line scales 73 (71-77) The lower jaw is usually equal to the upper

Coloration is like that of other species of cisco, but paler Pigment is usually present on all the fins, though sometimes the anal and ventrals are immaculate The snout may be so strongly pigmented as to appear black, a characteristic of typical *L reighardi* and of many typical examples of *L kiyi*

A form of *Leucichthys artedi*, probably *sargenti*, is also found in the lake *L bartletti* is distinguishable from this by having a reduced number of gillrakers, a much longer snout and much less body depth It also undoubtedly lives in much deeper water and probably grows larger

Leucichthys bartletti resembles *L zenithicus* and *L kiyi*, both of which occur in Lake Superior half a mile away It differs from both in having fewer gillrakers on the first branchial arch, from the former it is distinguished also by having the lower jaw equal to the upper and in having the pectoral fins a trifle longer From *kiyi* it differs chiefly in having the paired fins shorter Those characters that can be expressed numerically are compared below for the three forms All specimens are under 200 mm long

GILLRAKERS ON THE FIRST BRANCHIAL ARCH

SPECIES	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46
bartletti			5	3	1	4									
kiyi					3	8	11	13	23	7	7	3	1	1	
zenithicus	1	1	1	6	15	24	15	11	18	6	5	1		1	

PV/P

SPECIES	1 1	1 2	1 3	1 4	1 5	1 6	1 7	1 8	1 9	2	2 1	2 2	2 3	2 4
bartletti					2	4		1						
kiyi	1	10	15	24	20	6	2							
zenithicus				1	7	12	20	34	33	36	14	8	4	1

AV/V

Species	09	10	11	12	13	14	15	16	17
bartletti				3		3	3		
kiyi	1	23	34	15	5	1			
zenithicus		3	12	16	32	33	16	2	1

Two specimens, 145 and 146 mm long, have been found to be immature The rest (146 mm and larger) are mature The spawning time is after late summer, since none of the specimens taken had ripe eggs or recently spent ovaries

Coregonus clupeaformis (Mitchill)

The type-locality is falls of the St Mary's River Koelz, 1929, has shown that the Great Lakes whitefish is singularly constant in its characters, virtually the only variation noted being in depth of body A very marked structural change, however, was produced in all specimens reared from eggs to maturity in the New York Aquarium The results were duplicated exactly by the Ontario Game and Fisheries Department (See Figs 1 and 3 in *Report* for 1927 A specimen of this brood is in the collection of the Museum of Zoölogy)

All but one of the inland-lake forms so far known are different from the typical form that predominates in the Great Lakes In all the systematic characters usually employed one or other of these races varies from the typical *clupeaformis* in the same direction and to the same degree as did the artificially reared individuals, except for the broad blunt snout Inland-lake fish, even though they may be as short-snouted as the aquarium fish, have this part of normal shape

Seven forms are recognized Their characteristics are abstracted in the following analyses

The distribution of the subspecies is not more regular than that of the races of *Leucichthys artedi* It is noteworthy, however, that the species is by no means so generally distributed as the cisco, and apparently its range does not extend as far south.

Virtually nothing is known of the habits of the various races, but there are indications that they are as plastic in behavior as in structure Though Great Lakes forms have been found to be bottom feeders, subsisting chiefly on molluscs and crustaceans, the race of Lake Desor has been found to be heavily predatory on fish, fish believed to be of this species were frequently seen jumping in the evening, presumably for flies There is nothing to indicate that any of the races spawn at different times from the known breeding season in the Great Lakes

As in the case of *Leucichthys artedi*, the range in size at maturity is very great In certain Great Lakes populations (*Coregonus c clupeaformis*) maturity is not attained before the individual weighs three pounds, but in *Coregonus c gulliveri* mature fish are known 127 mm long, weighing less than an ounce

ANALYSES OF THE SUBSPECIES OF *COREGONUS CLUPEAFORMIS*

- A^1 Gillrakers chiefly 26 or fewer, lateral line scales usually fewer than 84
  - 1 L/H usually 4 5–4 8, PV/V usually less than 1 7 — *stanleyi*
- A^2 Gillrakers chiefly 26–28 except in *medorae* (27–32)
  - B^1 Lateral line scales usually 80–88 L/H usually more than 4 3
    - C^1 PV/P usually 1 7–2
      - 2 L/D in fish under 250 mm usually 4–4 5, in larger fish usually 3 8–4 3 — *clupeaformis*
      - 3 L/D in large fish 3 3–3 6 — *latus*
    - C^2 PV/P usually 1 4–1 7
      - D^1 L/H usually less than 4 8 in specimens under 250 mm
        - 4 L/D about intermediate between 2 and 3 — *neo-hantoniensis*
      - D^2 L/H usually more than 4 7 in specimens under 250 mm
        - 5 L/D as in 4 — *medorae*
  - B^2 Lateral line scales 84–97, L/H usually less than 4.4
    - 6 L/D usually 4 5–5 in all fish — *dustini*
- A^3 Gillrakers chiefly more than 28
  - 7 Body rather deep paired fins long — *gulliveri*

Coregonus clupeaformis stanleyi (Kendall)

The type is a male specimen 222 mm long, Cat no 50828, U S National Museum, taken in the Cross Lake Thoroughfare, Fish River Lakes, Maine Kendall, 1904, found two forms in the lake, one spawning at 165 mm and one attaining a weight of 5 lb

He found them apparently alike in other characters, but named the small form I have examined 24 fish from the type-locality, most of them taken by Dr Kendall on November 9, 1903 All are adult, spawning fish and measure 159–204 mm These small fish are different from *Coregonus clupeaformis* of the Great Lakes principally in having fewer gillrakers and lateral line scales and longer paired fins A single large fish, 317 mm long, that has been seen from this locality is like the small ones (typical *stanleyi*) in these respects its gillrakers number 24, lateral line scales 80, PV P is 1 5 It is possible that there are two species of *Coregonus* in one of the lakes, but I believe it more likely that there are two races that, even though they spawn on the same grounds, at least occupy different habitats during the rest of their lives, and *stanleyi* is tentatively made a subspecies of *clupeaformis* A detailed comparison of the number of gillrakers and lateral line scales and the L/H and PV/P ratio is given in Tables XXXVIII–XLI for the forms of *Coregonus*

Cross, Eagle and Square lakes (see below) are of the Fish River chain in Aroostook County, Maine

Penobscot River

Three immature individuals, 132–142 mm long, have been examined from the Penobscot River, taken in smelt seines in brackish water at Winterport, Maine, on March 26, 1917 They differ from *C c stanleyi* in having shorter pectorals (PV/P = 1 7, 1 7, 1 8), but provisionally are classed under that name

Three adult specimens from the collection of the Museum of Comparative Zoology, labeled "Maine," measuring 268–288 mm, may be considered typical *stanleyi* also

Telos Lake

Two immature fish, 178 and 193 mm long, have been examined from Telos Lake, Maine They may be regarded as *stanleyi*

Eagle Lake

An adult male, 188 mm long, has been seen from Eagle Lake It is apparently like *stanleyi*

Square Lake

Two specimens, an immature female 145 mm long and an adult male 170 mm long, have been seen from Square Lake Apparently they are very much like *stanleyi* in their characters

Coregonus clupeaformis clupeaformis (Mitchill)

Twelve specimens, 209 to 292 mm long, all immature, taken in 50-75 feet of water during August, 1923, have been examined from Torch Lake For other data pertaining to these captures see the account of *Leucichthys artedi greeleyi* on page 313

These fish are very close to the Great Lakes whitefish in all their characters

Coregonus clupeaformis latus, new subspecies

The whitefish of Lake Erie and of Black Bay in Lake Superior differ from typical *clupeaformis* principally in having greater body depth The name *C albus* has generally been applied to these fish, but Koelz, 1929, finds this name applicable to another species and it is here suggested that the Lake Erie form be named *latus*

A female specimen 376 mm long, Cat no 52805, Museum of Zoology, may be considered the type Its principal characteristics are given in Table 93, p 628 of Koelz, *Coregonid Fishes of the Great Lakes, Bureau of Fisheries Document 1048* Seventeen paratypes 291-402 mm long are preserved For comparison with other races of *Coregonus clupeaformis* see Tables XXXVIII-XLI

Walnut Lake

Nineteen specimens, chiefly adult, measuring 287 to 403 mm, taken by Professor T L Hankinson in April and May, 1906, are much like typical *latus*, except that the pectorals are a trifle long (PV/P is usually 1 6-1 8 as compared with 1 7-1 9 for *latus* and the body depth is rather less (L/D is 3 4-3 9 and 3 3-3 6, respectively) In the first character the race approaches *neo-hantoniensis* (about 1 5-1 7)

Coregonus clupeaformis neo-hantoniensis (Prescott)

Most of the various inland-lake races differ from the typical one chiefly in having relatively longer pectorals Prescott's old name for the Winnepesaukee Lake form *neo-hantoniensis* is probably applicable to *Coregonus* of this type, to judge from a single specimen, an adult female, 249 mm long, examined from the collection of the Museum of Comparative Zoölogy It is of course possible that Richardson's *labradoricus* from the "Musquaw River, Gulf of St Lawrence," will be found to be like these fish and that name has priority

The type is not known to be extant The type locality is Lake Winnepesaukee, New Hampshire Comparisons in certain characters of the races of this form with those of other subspecies of *C clupeaformis* are given in Tables XXXVIII-XLI

Otsego Lake

Nine specimens, 198–313 mm long, have been seen from Otsego Lake, taken February 2, 1911 Four specimens, 237 mm or less, are immature They differ from typical *clupeaformis* chiefly in having longer pectorals and hence are probably like *neo-hantoniensis*

Otsego Lake is a long narrow lake in Otsego County, New York, draining through the Susquehanna

Beau Lake

Three specimens from Beau Lake, measuring 153, 172 and 187 mm , taken on October 11, 1905, are apparently like *neo-hantoniensis* The smallest fish is an adult female, so that the race is undoubtedly dwarfed

Beau Lake, according to the label accompanying the specimens, is on the boundary between New Brunswick and Maine, a part of the St Francis River

Glasier Lake

Two fish, 200 and 201 mm long, both immature, taken October 12, 1901, are apparently like *neo-hantoniensis*

Glasier Lake, according to the specimen label, is a tributary of the St Francis River

Umsaskis Lake

Two fish, 98 and 130 mm long, taken October 3, 1901, are apparently like *neo-hantoniensis* The larger fish, though not adult, shows enlarging ovaries, so that the race is undoubtedly dwarfed

Umsaskis Lake is in Aroostook County, Maine, on the boundary of Piscataquis County It drains through the Allegash to the St Francis River

Lake Champlain

A single fish, 385 mm long, taken on July 2, 1929, by the New York Conservation Commission, is apparently like *neo-hantoniensis*

A brief description of Lake Champlain is given on page 339

Lake Chazy

An adult male, 297 mm long, taken by the New York Conservation Commission on July 22, 1929, is apparently like *neo-hantoniensis*

Lake Chazy is a rather regularly elongate lake in Clinton County, New York, about ¾ mile long with a maximum width of about 1 mile John R Greeley says the maximum depth is about 40 feet

Lake Kiwassa

Three fish, 325–330 mm long, taken by the New York Conservation Commission on August 7, 1929, are like *neo-hantoniensis*

Lake Kiwassa is in Franklin County, New York It is rather regularly elongate, with maximum dimensions of 1½ by ¾ miles Mr Greeley gives the greatest depth as about 30 feet

Lake Clear

Two adult males, 292 mm long, taken by the New York Conservation Commission on October 30, 1929, are apparently like *neo-hantoniensis*

Lake Clear is in Franklin County, New York It is a regularly elongate body of water measuring about 1 by 2 miles Mr Greeley gives the maximum depth as about 50 feet

Eagle Lake

A specimen, immature, 198 mm. long, taken by the New York Conservation Commission on July 11, 1929, is short-finned (PV/P = 1.8), like typical *clupeaformis*. It may, however, be only an extreme example of *neo-hantoniensis*, the common form of the region.

Eagle Lake is an irregularly elongate lake, 2¾ miles long, with a maximum width of less than ½ mile, in Essex County, New York.

Saranac Lakes

Seven specimens, 295–449 mm. long, chiefly adult, were taken by the New York Conservation Commission in July and August, 1929, in Upper Saranac, and one 321 mm. long, immature, from Lower Saranac. All appear to be like *neo-hantoniensis*. The Saranac Lakes are in Clinton County, New York. Both are very irregular in outline with numerous bays and islands. The Upper Lake is about 7½ miles long, the Lower about 5 miles.

Lake Simcoe

An adult female, 342 mm. long, and two immature specimens, 226 and 310 mm. long, from the Ontario Game and Fisheries Collection, apparently are *neo-hantoniensis*.

For location of Lake Simcoe see page 326.

Lake Mindemoya

Spawning females, 322 and 367 mm. long, taken by me on November 12, 1917, apparently belong to this form.

For location of this lake see page 352.

Upper St. Mary's Lake

Six specimens, 337 to 350 mm. long, chiefly adult, taken by Dr. A. Murie on September 7, 1927, appear to be *neo-hantoniensis*.

Upper St. Mary's Lake is a rather regularly elongate lake about 10 miles long and 1 mile wide, in Glacier National Park. It drains into the Saskatchewan River.

Siskowit Lake

Twenty-three specimens, 165–313 mm long, and two, 361 and 365 mm long, have been examined, taken by me August 21–25, 1929, in 50–117 feet of water in Lake Siskowit Only the two largest fish are adult They are much like other inland lake whitefish except that the maxillary appears to be a trifle longer, relatively, but this character cannot easily be recorded in a fish with so soft a snout, and the form may be known as *neo-hantoniensis*

The location and physical features of this lake are given on pages 331–333

Stone Lake

Twenty adult specimens, 175 265 mm long, taken by the Wisconsin Geological Survey, appear to have a relatively slightly larger head and eye than the usual inland-lake form, but this difference may be due to the smaller size of these fish and they are therefore considered *neo-hantoniensis*

Stone Lake is in Forest County, Wisconsin Its maximum dimensions are 0 7 by 3 5 miles and its area 1 32 square miles, or 844 8 acres The greatest known depth is 76 4 feet Drainage is into Green Bay

Wabigoon Lake

A specimen from the U S National Museum, number 64724, 275 mm long, may be grouped here

A brief statement about this lake is given on page 367

Athabaska Lake

Five specimens from this lake, measuring 300–408 mm, are apparently referable to *neo-hantoniensis*

Lake Athabaska is about 195 miles long, with a maximum breadth of 35 miles and an area of 3,000 square miles No soundings are known (Murray, 1910)

Granite Lake

Four fish from the Ontario Game and Fisheries Collection, taken in Granite Lake, are apparently *neo-hantoniensis* Two are immature, 210 and 221 mm long, and two adult, 248 and 362 mm long

Granite Lake, according to the specimen label, is in the District of Kenora, Ontario

Upper Stony Lake

Two specimens, 208 and 272 mm long, from the Ontario Game and Fisheries Collection, taken on June 27, 1929, are apparently of the race *neo-hantoniensis*

Upper Stony Lake is in Peterborough County, Ontario

Thames River

Eight specimens, 190–258 mm long, from the Ontario Game and Fisheries Collection, apparently belong to the race *neo-hantoniensis*, except that they are rather deeper-bodied L/D is 3 4–3 9 for specimens over 200 mm Four specimens are immature, measuring under 235 mm , those above that limit are adult

The label says that these fish were taken from a box containing "trout, white bass, perch, pickerel", they probably originated in the Thames River, Ontario Presumably the lot was confiscated

Coregonus clupeaformis medorae, new subspecies

The type is a female specimen, 270 mm long, Cat no 96973, Museum of Zoölogy, collected by Professor John N Lowe in Lake Medora on August 19–20, 1927 Twenty-four paratypes, taken at the same time, measure 165–272 mm Most of them are adult

This race is distinguished from typical *clupeaformis* chiefly in having longer pectorals, deeper body and smaller head It has also a few more gillrakers on the first branchial arch. None of the other described races of *C clupeaformis* is known to have so small a head and the form is therefore named as new Many individuals are further distinguished by having the mandible projecting beyond the premaxillaries Comparison of several characters with other subspecies of *C clupeaformis* is given in Tables XXXVIII–XLI

Medora Lake

Medora or Mosquito Lake is in the northeast part of Keweenaw County, Michigan It is about 2 miles long with a maximum width of about ¾ mile It drains through the Montreal River into Lake Superior Professor Lowe says the lake is shallow (maximum depth 20 feet), and has a bottom of chiefly hard sand and rock

Coregonus clupeaformis dustini, new subspecies

The type is a female specimen, 314 mm long, Cat no 96972, Museum of Zoölogy, caught on September 10, 1929, in Lake Desor Twenty-seven paratypes, measuring 172–314 mm long, taken at about the same time, have been examined for this description Those under 290 mm are immature The smallest mature fish of both sexes weigh about half a pound

The whitefish are extraordinarily abundant in the lake, as is evidenced by the fact that a piece of 2½-inch net, about 200 feet long, set in 5-21 feet on September 8 at 8 P M and lifted on September 10 at 9 A M took 116 whitefish, a piece of 2-inch net in the same gang, but in 30-40 feet of water, got 18 (temperature in 30 feet, 17 2° C)

This form is distinguished from typical *clupeaformis* by having slightly more lateral line scales and proportionally a much longer head, maxillary and pectorals The body depth is also much less Comparisons of several characters are given for the various races of *clupeaformis* in Tables XXXVIII–XLI

The food of many specimens was examined Of a total of 117 individuals, 30 had eaten nothing, 51 had eaten only fish, never more than two (nine-spined stickleback, 17, Cottus, 5, herring 3 and 4 inches long, 2, unidentifiable, 27) Seven others had eaten fish and incidentals such as sticks, gravel, balsam needles, stinkbug, juvenile Corixa, Pisidium, maple keys The 29 remaining fish had a mixed diet flywing, 3 one-half inch moths, very fresh, gravel and cedar leaves (4 fish), gravel (4 fish), 1 and 4 burrowing mayfly nymphs (3 individuals), 1 Physa, 3 Pisidium (2 individuals), 12 water mites, midge larvae, 1 juvenile Corixa, piece of sponge, piece of $CaCO_3$ from a clam shell, piece of wood 2 cm long (3 individuals), one-inch stick, piece of bark, cedar leaf, gelatinous alga colony, piece of Potamogeton stem 3 inches long (2 individuals), granite pebble one-half inch in diameter (2 individuals), cedar leaf (2 individuals)

A brief description of Lake Desor is given on page 318

Trout Lake

Fifty-four specimens taken by Dr Wright in the summer of 1927 and by the Wisconsin Natural History Survey on November 12, 1906, have been examined from Trout Lake Of these 17 are over 275 mm long and are adult, most of the rest are under 200 mm long and are immature These fish differ from typical *clupeaformis* in the same characters and in the same degree as *dustini*, except that the lateral line scales are no more numerous, nor is the body depth less The last-named character may be influenced by nutrition

A statement of the location and physical features of Trout Lake may be found on page 350

Coregonus clupeaformis gulliveri, new subspecies

The type is a male specimen, 224 mm long, Cat no 96974, Museum of Zoölogy, collected in Gulliver Lake in December, 1917 Four paratypes, 218–395 mm long, all adult, have been examined from the same catch The form differs from typical *clupeaformis* principally in having more gillrakers and longer paired fins It probably will be found to have also relatively larger eyes A detailed comparison of several of these characters is given in Tables XXXVIII–XLI for the various forms of *Coregonus*

Gulliver Lake

Gulliver Lake is in southwestern Schoolcraft County, Michigan, and drains into Lake Michigan

Allegash River, Maine

A mature female, 127 mm long, collected by Kendall and Goldsborough at Old Burnt Dam on the Allegash River on September 23, 1901, has 31 gillrakers, 76 lateral line scales and 1 4 for PV/P It may, therefore, be classed with *gulliveri*

Lake Chateaugay

Eight adult specimens, 165–191 mm long, have been seen from Lake Chateaugay Apparently they are like *gulliveri*, but seem to have fewer lateral line scales than *clupeaformis* If *gulliveri* is found to be like *clupeaformis* in the matter of scale count, then the Chateaugay fish may be separable from both These fish are apparently dwarfs, since they spawn so small

The label does not say in which of the Chateaugay lakes the specimens were caught Both are large lakes in northeastern New York

Sturgeon

A specimen, 212 mm long, taken on June 19, 1927, by the Ontario Game and Fisheries Department, has 32 gillrakers and is thus like *gulliveri*

Sturgeon Lake is in Peterborough County, Ontario

Chicogan Lake

A single fish, taken on July 1, 1928, by Professor Lowe, is apparently like *gulliveri*

Lake Chicogan is an irregularly elongate lake near the southern border of Iron County, Michigan It is nearly 3½ miles long with a maximum width of 1 mile Professor Lowe says the lake is reported to be 75–80 feet deep It drains through the Menominee River into Lake Michigan

Other lakes

Two specimens from the Field Museum Collection measuring 318 and 330 mm, collected at Chapleau, Ontario, two, 290 mm long, from Athabaska River and one, 368 mm long, from the Saskatchewan River, all from the Museum of Comparative Zoölogy, three from Island Lake, Cook and Lake counties, Minnesota, are deeper-bodied than *neo-hantoniensis*, but otherwise apparently the same The values for L/D are 3 1, 3 2 3 1, 3 2, 3, and 3 2, 3 2, 3 4, respectively

Lacking more specimens, I find it inadvisable to name these fish

Prosopium quadrilaterale (Richardson)

The type is from "small rivers about Fort Enterprise and in the Arctic Sea " There are known specimens from this area, but Koelz, 1929, assumes that the Great Lakes races of *Prosopium* are very like them and the name may for the present at least be used for the Great Lakes forms

Specimens have been examined as follows from New Hampshire a specimen each from Lake Village and Newfound Lake (Museum of Comparative Zoology), measuring 270 and 307 mm , respectively, from Maine two adults from Umsaskis Lake, 193 and 218 mm , and ten adults, 209–246 mm long, from Cross Lake Thoroughfare, Aroostook County, from New York a specimen from Mirror Lake, 353 mm long, two from Clear Pond off Rainbow Lake, one from Big Clear Lake, 311 mm long, three from "lake in Adirondack Mountains", and twenty specimens, 179–223 mm long, from Lake Chazy

Probably none of the inland-lake *Prosopia* will be found to be exactly like the races of the Great Lakes If *P quadrilaterale* of Lake Michigan is taken as a representative of the typical form, virtually all these inland races appear to differ from it in having longer paired fins and fewer lateral line scales Cross Thoroughfare and Chazy Lake specimens apparently differ further in having relatively a somewhat larger head and Chazy Lake fish differ still more in having fewer gillrakers on the first branchial arch The latter is selected as the type of the form

Prosopium quadrilaterale minor, new subspecies

The type is a female specimen, 202 mm long, Cat no 96975, Museum of Zoölogy, taken by J R Greeley on July 22, 1929, in Lake Chazy Nineteen paratypes, 179–223 mm long, virtually all near to sexual maturity, were taken at the same time, data for all these specimens, as well as for the other inland-lake forms and for the Lake Michigan one, are given in Tables XLII-XLV The form differs chiefly in having slightly fewer lateral line scales and gillrakers on the first branchial arch, and relatively a somewhat larger head and paired fins As in Great Lakes specimens of comparable size, parr-marks are still evident on the back, down to the lateral line in the caudal area

Other species

To the list of the coregonid fauna of northeastern America should be added the forms given for the Great Lakes by Koelz, 1929 *Leucichthys johannae* (Wagner), *L alpenae* Koelz, *L zenithicus* Jordan & Evermann, *L reighardi reighardi* Koelz, *L reighardi dymondi* Koelz, *L nigripinnis nigripinnis* (Gill), *L nigripinnis cyanopterus* (Jordan & Evermann), *L nigripinnis regalis* Koelz, *L nigripinnis prognathus* (Smith), *L kiyi kiyi* Koelz, *L kiyi orientalis* Koelz, *L hoyi* (Gill), *L artedi artedi* (Le Sueur), *L artedi albus* (Le Sueur), *L nipigon* Koelz, *Coregonus clupeaformis* (Mitchill) and *Prosopium quadrilaterale* (Richardson) *Leucichthys hubbsi* Koelz occurs in Ives Lake, Marquette County, Michigan

Several of the Great Lakes species exhibit in their range races morphologically well marked, but these have not been named, because it is felt that too few data have been accumulated for an adequate treatment of raciation in the Great Lakes coregonids It is hoped that some student will undertake this study in the future What has so far been done is but an introduction to a problem that will yield through study results of far-reaching significance

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In Koelz 1929, is given a more or less complete list of the literature dealing with the coregonid fauna of the Great Lakes area There have been numerous notes recording the occurrence of some coregonid form in the area treated in this paper, but these notes have in the main attempted to give no analysis of their specimens which cannot therefore be identified, and such works are not mentioned here In Adams and Hankinson, 1929 will be found a long bibliography which includes some of these references Only those authors that have been quoted in the preceding pages are therefore listed here, except that the list includes works of any character that deal with coregonids that have appeared since the preparation of the bibliography for the Great Lakes region

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TABLE I

Frequency Distribution of the Number of Gillrakers on the First Branchial Arch for the Type Races of the Various Subspecies of *Leucichthys artedi*

Subspecies	31	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	5
artedi									1	2	7	18	24	46	57	62	49	37	44	22	14	4	4				
osmeriformis															1	2	4	1	3			1	1				
lowei														4	3	10	10	20	11	6	6						
clarensis												1	2	5	5	9	9	4	3	1			1				
sisco											2	1	4	3	8	8	1	1	2								
microcephalus												8	2	1	1	2	1										
albus									2	5	23	32	37	56	58	40	41	17	3	1	2						
huronicus									2	5	6	4	3														
clemensi									1	1		2	4	10	14	11	14	5	6	2	1						
annensis								1	8	3	5	6	10	7	3												
bergei									2	2	10	6	8	4	3	2											
russeli									1	4	13	24	23	16	11	6	5		1	1							
greeleyi	1	1	2	2	1		7	8	14	15	9	4	5	1													
atikamek												2	1	2	1		1										
sargenti							1	1	1	1	1	3	1														
wagneri																1	1		1	2			2	1			
manitoulinus											1	3	3	4	6		1		1								
hankinsoni									1	2	1	1	1	2	2	1											
tullibee																	1	1	1		2	1					
mendotae														1	2	2	5	2	1	2	1	1					
woodi														1	3	5	2	3	1								
winnipegosis												1		2	1	3	2										
magnus												2	1	1					1								
mackayi												3	1	7	8	3			2								

Note — For size of specimens compared see note to Table III

TABLE II

Frequency Distribution of the Number of Lateral Line Scales for the Type Races of the Various Subspecies of *Leucichthys artedi*

Subspecies	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94
artedi								1			1	1	3	2	6	13	15	15	19	24	40	37	38	29	40	24	20	13	14	5	4	2	4	1
osmeriformis																	1	1	1	1	1	2	1		2	1			1					
lowei													1		1	4	5	3	6	11	8	4	8	8	1	4	3			2	1	1		
clarensis										1				1	1	1	1	7	6	4	7	6	4	3		2		1						
saco													1	1		1	2	4	2	8		1	3	1					1					
microcephalus																		1		1		1	1	3	1	1			1					
albus				1		2	3	1	17	22	35	48	64	80	76	97	74	66	47	35	31	14	12	9	7	2		1	1					
huronicus													3	2		3	2	1	5			1	1	1										
clemensi					1			3	4	5	9	7	6	10	6	8	3	4	3	2	1													
annensis														2	3	4	3	3	3	4	1	3	7	3	4			1						
bergei										1	4	2	4	5	7	5	4	2	1	1		1												
russeli										2	1	5	4	16	10	14	10	7	10	9	4	4	3	2		1								
greeleyi											1		3	1	2	3	5	6	6	7	3	2	6	6	5	2	4	4	2	1				
atikamek							1				1	2	1	1		1	1																	
sargenti					2						2	1			1		1																	
wagneri								2				1	1	4	1																			
manitoulinus									1	1	3	1	2	4	1	4	2				1													
hankinsoni	2		1			2	3	3			1	1																						
tullibee								1		1				1	1			1	1															
mendotae						1					4	3	3	3		2	1		1															
woodi							1		2	1		1	2	3		3	2																	
winnipegosis		1	1	4	1		1		1																									
magnus											1				1	1	1	1																
mackayi										1		1	2	3	3	2	2	1	1	1				1		1								

TABLE III

FREQUENCY DISTRIBUTION OF THE RATIO BETWEEN BODY LENGTH AND HEAD LENGTH (L/H) FOR THE TYPE RACES OF THE VARIOUS SUBSPECIES OF *Leucichthys artedi*

SUBSPECIES	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57
artedi					1	13	25	35	32	15	10	5		2							
do *				5	14	30	36	32	21	8											
cameriformis				1	1		3	4	1	1	1										
lowei *					12	24	21	5	2	4											
clarensis *				2	7	11	11	4	3	3	3	1									
sisco									1	2	4	5	7	3	2						
microcephalus														2	3	1	2				1
albus					1	4	15	20	35	31	26	13	4	5							
do *			1	5	10	30	40	26	5	3	2										
huronicus *			1	7	6	1	1	1													
clemensi		1		3	3	3	2	1													
do *			1	5	11	19	19	6	6	1											
annensis *				1	1	1	4	9	15	7	3										
bergei				3	10	13	6	3	1	1											
russeli					3	9	6	1	1												
do *	1	7	13	13	21	12	13	5													
greeleyi				2	8	12	7	4	1												
do *	1	7	7	2	12	4	3														
atikamek					1	4	3														
sargenti *	2	3	1	2																	
wagneri *				6	[illegible]	1															
manitoulinus			2	7	5	4	2														
hankinsoni				1	4	4	1														
tullibee				1	2	2	1														
mendotae		1		1	3	8	4	1													
woodi			1	1	5	4	2	2													
winnipegosis *	4	1	1	3																	
magnus		2					2	1													
mackayi *			3	3	5	4	2														

* The asterisk (*) indicates that the specimens are chiefly under 225 mm long all others are over that limit except *atikamek* of which the number above is only half Specimens of *sisco mendotae* and *magnus* are over 260 mm *Huronicus mackayi* and *clarensis* are chiefly under 200 mm and specimens of *sargenti* are under 125 mm

TABLE IV

FREQUENCY DISTRIBUTION OF THE RATIO BETWEEN VENTRAL-ANAL DISTANCE AND LENGTH OF VENTRAL FIN (AV/A) FOR THE TYPE RACES OF THE VARIOUS SUBSPECIES OF *Leucichthys artedi*

SUBSPECIES	1 1	1 2	1 3	1 4	1 5	1 6	1 7	1 8	1 9	2 0	2 1	2 2	2 3	2 4
artedi				1	13	18	48	31	18	8		2	1	
			2	7	27	50	37	11	5	1				
osmeriformis			1	1	8	3	3	1						
lowei		2	6	24	25	12	1							
clarensis				2	10	18	8	3	2	2				
sisco							1	6	10	6	1		1	
microcephalus							1	1	1	1	3		1	1
albus				6	28	35	33	16	16	8	2			
			7	32	40	28	2	3						
huronicus			1	5	9	3	1							
clemensi				5	4	3	1							
			2	8	22	27	6							
annensis			1		2	7	10	7	1					
birgei	1	3	9	10	9	3	1							
russeli				1	9	2	6	1	1					
		1	6	17	23	19	17	4						
greeleyi					1	11	14	8						
		1	4	5	9	8	7	1	1					
atikamek			1	2	2	3								
sargenti		1	8	2	1									
wagneri			1	1	6	1								
manitoulinus	1	1	7	6	3	2								
hankinsoni				3	3	3	2							
tullibee		1		1	2									
mendotae				1	5	5	2	2	1					
woodi		1		2	5	4	3							
winnipegosis	1	8	2	2										
magnus	1	2	2		6									
mackayi			2	7		3	1							

Note — For size of specimens compared see note to Table III

TABLE V

Frequency Distribution of the Ratio between Pectoral-Ventral Distance and Pectoral Length (PV/P) for the Type Races of the Various Subspecies of *Leucichthys artedi*

Subspecies		1 1	1 2	1 3	1 4	1 5	1 6	1 7	1 8	1 9	2 0	2 1	2 2	2 3	2 4	2 5
artedi	+ 225						1	2	5	24	35	24	24	14	4	5
	− 225						3	5	20	23	57	21	10	1	1	
osmeriformis							1	1	1	1	5	3				
lowei						4	14	25	22	6						
clarensis						3	7	14	7	5	4	1	[illegible]	1		
sisco												5	8	11	1	
microcephalus												6		2		1
albus	+ 225						2	12	1	26	37	25	17	8	6	3
	− 225						8	17	37	30	25	4	1			
huronicus							5	3	6	5						
clemensi	+ 225						2	7	4							
	− 225					3	13	23	18	5	4					
annensis							2	3	4	7	9	2	2			
birgei						2	3	11	8	7	4	2				
russelli						5	14	16	18	29	8	11	5	2	2	
greeleyi	+ 212									5	8	11	8	2		
	− 212							6	7	8	9	3	1	1		
atikamek						1	3	4								
sargenti				4	1	2	1									
wagneri					1	3	3	2								
manitoulinus						1	9	7	2							
hankinsoni						1	1	4	3		2					
tullibee					1		1	1								
mendotae						3	4	3	3	1		1				
woodi					1	3	8	2		1						
winnipegosis			1		4	2	1									
magnus		1		2	1	1										
mackayi					3	5	4	2	4	1						

Note — For size of specimens compared see note to Table III

TABLE VI

FREQUENCY DISTRIBUTION OF RATIO BETWEEN LENGTH OF HEAD AND SNOUT (H/S) FOR THE TYPE RACES OF THE VARIOUS SUBSPECIES OF *Leucichthys artedi*

SUBSPECIES	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
artedi	2		3	16	24	30	19	26	5	5	1	1				
		2	8	24	40	36	20	12	2							
osmeriformis			1	1	1	6		2		1						
lowei			3	7	16	6	7	8	3	1						
clarensis					1	7	6	12	8	4	5	2				
sisco						1	4	7	4	3	4		1			
microcephalus								2	2	3	1			1		
albus				4	12	24	27	40	10	5	4	2	1	1		
				15	25	22	24	32	9	1						
huronicus						3	4	4	6							
clemens			1	1	6	2	2		1							
				3	10	14	12	9	6	3						
annensis					3	5	9	6	1	4	1					
birgei		3	7	13	9	4		1								
russelli			1	1	3	7	5	3								
			1	9	14	31	18	7	4	1						
greeleyi		1	4	11	10	7	1	1								
			5	5	4	7	12	2	1							
atikamek							1	2		2	1	2				
sargenti						2			1	2	1	1				
wagneri							2	1	1	2	2		1			
manitoulinus					3	4	3	8		1	1					
hankinsoni						1			1	2	1	1	3	2		
tullibee						1		3		1		1				
mendotae							1	3	2	1	4		3	1		1
woodi						1		2		5	2	2				
winnipegensis									1	[illegible]	1	2	2		1	
magnus						1		3		1		1				
mackayi						3	3	5	2	2	1					

Note — For size of specimens compared see note to Table III

TABLE VII

Frequency Distribution of the Ratio between Length of Head and Maxillary (H/M) for the Type Races of the Various Subspecies of *Leucichthys artedi*

Subspecies	2 3	2 4	2 5	2 6	2 7	2 8	2 9	3 0	3 1	3 2	3 3	3 4	3 5
artedi			5	7	21	37	36	21	3	2	1		
		1	3	16	39	44	23	17	2				
osmeriformis			1	4	2	4			1				
lowei				2	14	30	16	7	2				
clarensis						1	11	16	10	4	3		1
sisco							4	8	6	6			
microcephalus								2	3	3	1		
albus			3	16	40	42	21	15	2	3	1		
			3	27	40	28	10	1	1				
huronicus					1	3	7	4	1	1			
clemensi			1	3	5	3	1						
				7	26	30	2	2					
annensis				2	3	15	7	2					
birgei		5	13	8	9	2							
russelli				1	2	6	8	2	1				
			1	6	25	32	15	3	2		1		
greeleyi				2	5	14	10	2	1				
	1	1	5	4	5	11	8	1					
atikamek					1	2	2	2	1				
sargenti				4	3								
wagneri					1		1	1	6				
manitoulinus			2	5	7	6							
hankinsoni								3	5	1	1	1	
tullibee						2	2	2					
mendotae							2	4	3	7	1		1
woodi							3	7	2		2		
winnipegosis						3	1	3	2				
magnus					1	1	1	1	1				
mackayi				3	5	7	3						

Note — For size of specimens compared see note to Table III

TABLE

FREQUENCY DISTRIBUTION OF RATIO BETWEEN BODY LENGTH
SUBSPECIES OF

SUBSPECIES		27	28	29	30	31	32	33	34	35	36	37	38	39
artedi	+ 225										2		2	7
	− 225													
osmeriformis														
lowei														1
clarensis	+ 225											2	2	2
	− 225													
sisco												3	3	6
microcephalus									1		2	4	2	
albus	+ 225		2		6	7	5	19	21	12	19	12	5	7
	− 225		1		2		1	1	4	8	13	21	21	18
huronicus														
clemensi	+ 225											1		1
	− 225											2	1	4
annensis														
birgei							1		2	7	2	5	4	6
russeli	+ 225							1	1	3	3	4	4	1
	− 225								1	3	7	6	14	16
greeleyi	+ 212												1	
	− 212													
atikamek								2	3			2	1	
sargenti														
wagneri										2	3	2	1	1
manitoulinus									2	8	5	2	4	2
hankinsoni		1	3	1	8	2	2							
tullibee					1		2	1			2			
mendotae										1	8	3	1	3
woodi									1	3	2	3	5	
winnipegosis				1	1	1	4	1						
magnus			1		1	1	2							
mackayi														

Note — For size of specimens

VIII

AND BODY DEPTH (L/D) FOR THE TYPE RACES OF THE VARIOUS *Leucichthys artedi*

4 0	4 1	4 2	4 3	4 4	4 5	4 6	4 7	4 8	4 9	5 0	5 1	5 2	5 3	5 4	5 5	5 6	5 7	5 8
9	11	12	9	14	5	13	14	13	9	4	5	1	2					
	2	2	4	9	11	17	15	18	10	18	3	6	3	4	2	1	2	1
1		1		2	2		4	1					1					
1	6	10	15	13	9	9	6	1										
		2	2	3	1	3	8	1	3	4	1	2						
5	3	3		1		1												
4	5	1	1															
14	5	3	1															
1		1	1	1	1		1	2	2	4		1		1	3			
		4	1	1	1	2	2											
10	16	7	5	4	8	2	1	1	1									
1	1	2	3	1	2	5	4	4	1		1	1						
2			1	1														
7	5	3	4	5	8	1	3											
1		7	11	4	3	1	2		2									
				2	3	2	2	6	4	4	5	1	1	1	1			
		1	2	1						1								
1																		
3	3	1																
		1	1	4		2	2	2	1	2	1							

compared see note to Table III

TABLE IX

RANGE OF VALUES USUAL AND EXTREME FOR L/H AND I /D FOR SIX SUBSPECIES OF *Leucichthys artedi*

SUBSPECIES AND LAKE	L/H	I /D
greeleyi		
Torch *	(4) 4 1 4 4 (4 5)	(3 8) 4 2 4 5 (4 9)
	(3 7) 3 8–4 2 (4 3)	(4 4)4 8–5 1 (5 5)
Elk *	(3 9) 4 1 4 4 (4 6)	(3 8) 4 2 4 6 (5)
	(3 8) 3 9–4 2 (4 4)	(4 3) 4 5–5 1 (5 6)
Canandaigua	3 6 3 7 4	5 6,5 8
Keuka	3 7–4 1	(4) 4 5–5 1 (5 3)
Owasco	3 9 4 4 2	4 4 2, 4 8
George	(3 8) 4 4 2 (4 3)	4 8–5 (5 9)
Skaneateles	(3 9) 4–4 1 (4 2)	(3 8) 4 2–4 7 (5 3)
annensis		
Anne	(4) 4 3–4 6 (4 7)	4–5
huronicus		2
Rush	(3 9) 4–4 1 (4 4)	(4) 4 5–5 5
Desor	3 9 4 2	4 9–5 1
Chautauqua †	3 8	4 6,4 7
sargenti		
Sargent †	3 7–4	4 2–4 4
Richie †	3 8	4 5
atikamek		
Whitefish	4 1 4 3	3 3–3 8
Crawling Stone	4–4 2	3 5–4 4
russeli		
Pine *	4 1–4 3	(3 3) 3 5–4 (4 4)
	(3 7) 3 9–4 3 (4 4)	(3 4) 3 7–4 3 (4 7)
Twelve-Mile	(3 8) 4–4 2 (4 3)	3 9–4 8
Simcoe	(3 7) 4–4 3	(4) 4 5–5 (5 2)

* Data on species marked with an asterisk (*) are based on an examination of specimens principally over 225 mm long All other figures are based chiefly on fish under that limit

† Species marked with a dagger (†) are under 150 mm

TABLE X

FREQUENCY DISTRIBUTION OF THE NUMBER OF GILLRAKERS ON THE FIRST BRANCHIAL ARCH FOR SIX SUBSPECIES OF *Leucichthys artedi*

SUBSPECIES AND LAKE	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51
greeleyi																					
Torch	1			1	2	2	1		7	8	14	15	9	4	5	1					
Elk						5	6	9	16	22	24	34	26	22	12	3	4				
Canandaigua								2	1												
Keuka											1	3	1	2	2	3	1	1			
Owasco								1			1										
George								1	1	2	5	2									
Skaneateles									2	1	1	1	3		1						
annensis																					
Anne										1	3	3	5	6	10	7	3				
huronicus																					
Rush											2	5	6	4	3						
Desor											1			1	2						
Chautauqua															2						
sargenti																					
Sargent									1	1	1	1	1	3	1						
Richie										1			1		1						
alikamek																					
Whitefish														2	1	2	1		1		
Crawling Stone															2	1	1	2	1	1	
russeli																					
Pine											1	4	13	24	23	16	11	6	5		1
Twelve-Mile												1		2	2	2	1				
Simcoe											2	5	7	6	6		2				

TABLE XI

Frequency Distribution of the Number of Lateral Line Scales for Six Subspecies of *Leucichthys artedi*

Subspecies and Lake	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90
greeleyi																										
Torch							1		3	1	2	3	5	6	6	7	3	2	6	6	5	2	4	4	2	1
Elk					1	2	1	2	4	8	8	12	19	19	17	15	16	11	12	19	7	3	1	1		
Canandaigua								1		1			1													
Keuka								1				3		2	1		4		2						2	
Owasco									2																	
George							1	2		1	1			1	1		1	2	1							
Skaneateles							1	1		4	2			1		1										
annensis																										
Anne										2	3	4	3	3	3	4	1	8	7	3	4			1		
huronicus																										
Rush									3	2		5	2	1	5			1	1	1						
Desor												1		1			1									
Chautauqua.		1						1																		
sargenti																										
Sargent	2						2	1			1		1													
Richie										1																
atikamek																										
Whitefish			1				1	2	1	1		1	1													
Crawling Stone					2			1	2				1			1		1								
russeli																										
Pine						2	1	5	4	16	10	14	10	7	10	9	4	4	3	2		1				
Twelve-Mile							2		1	1	2			1		1										
Simcoe							1		4	2	6	4	3	3	5	1		1								

TABLE XII

FREQUENCY DISTRIBUTION OF THE RATIO BETWEEN THE LENGTH OF THE PECTORAL AND THE PECTORAL-VENTRAL DISTANCE (PV/P) FOR SIX SUBSPECIES OF *Leucichthys artedi*

SUBSPECIES AND LAKE	12	13	14	15	16	17	18	19	20	21	22	23	24
greeleyi													
Torch *								5	8	11	8	2	
do						6	7	8	9	3	1	1	
Elk *						2	6	20	14	12	5	1	1
do					2	10	27	34	17	18	6		
Canandaigua				1		1		1					
Keuka						1		1	6	5	2		
Owasco						1	1		1				
George							3	2	4	2	1		
Skaneateles					2	1	4		2				
annensis													
Anne					2	3	4	7	9	2	2		
huronicus													
Rush					5	3	6	5					
Desor					3								
Chautauqua †					1		1						
sargenti													
Sargent †		4	1	2	1								
Richie †	1												
atikameg													
Whitefish				1	3	4							
Crawling Stone				2	1	5			1				
russeli													
Pine *						4	3	9	1		1	1	1
do				5	14	12	10	20	7	11	4	1	1
Twelve-Mile				2	1	2	3						
Simcoe						2	7	6	4	1		1	

* † See notes to Table IX

TABLE XIII

FREQUENCY DISTRIBUTION OF THE RATIO BETWEEN HEAD LENGTH AND SNOUT LENGTH (H/S) FOR SIX SUBSPECIES OF *Leucichthys artedi*

SUBSPECIES AND LAKE	34	35	36	37	38	39	40	41	42	43	44	45	46
greeleyi													
Torch *	1	4	11	10	7	1	1						
do		5	5	4	7	12	2	1					
Elk *	1	6	13	19	8	15	2		1				
do		20	17	18	33	16	10	3	1	1			
Canandaigua		3											
Keuka			4	4	5	2							
Owasco		1		2									
George				5	2	2	3						
Skaneateles		1	3	5									
annensis													
Anne				3	5	9	6	1	4	1			
huronicus													
Rush						3	4	4	6				
Desor					1		1	1					
Chautauqua †								1	1				
sargenti													
Sargent †					2			1	2	1	1		
Richie †									1				
atikamek													
Whitefish						1	2		2	1	2		
Crawling Stone					1		1	2	1	1	1		1
russeli													
Pine		1	1	3	7	5	3						
do †		1	9	14	31	18	7	4	1				
Twelve-Mile			1		1	2	3	1					
Simcoe			3	3	1	5	5						

* † See notes to Table IX

TABLE XIV

FREQUENCY DISTRIBUTION OF THE NUMBER OF GILL-RAKERS ON THE FIRST BRANCHIAL ARCH FOR SEVERAL DEEP-BODIED SUBSPECIES OF *Leucichthys artedi*

SUBSPECIES AND LAKE	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56
tullibee																
Pine Island									1	1	1		2	1		
Winnipeg									4	3	2	3	2			
Lake of Woods			1				1	1	1		1	1				
Rainy										1						
Wakesiu							1				1	1				
winnipegosis																
Winnipegosis				1		2	1	3	2							
Wabigoon						2		1	1							
Otter						4		1								
Van Etten				1												
Portage							1									
Kenogami							1									
magnus																
Lesser Slave				2	1	1					1					
hankinsoni																
Oneida	1	2	1	1	1	2	2	1								
mendotae																
Mendota						1	2	2	5	2	1	2		1	1	
Hammills									1							
woodi																
N. Twin						1	3	5	2	3	1					
Whitestone									1	1						
Kawaguesaga			1			2	6	6	3	4	1	1	2	1	1	1
Long					1	1	1	2	2		1	1				
Shell							1									
Wolf											1			1		
Charter							1						1			
manitoulinus																
Typical form			1	3	3	4	6		1		1					

TABLE XV

Frequency Distribution of the Number of Lateral Line Scales for Several Deep-bodied Subspecies of *Leucichthys artedi*

Subspecies and Lake	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86
tullibee																													
Pine Island											1		1				1	1			1	1							
Winnipeg	1						2		2	1		2	1	4	1														
Lake of Woods												1	1	2	1	1		1	2										
Rainy														1															
Wakesu																					1	1					1		
winnipegensis																													
Winnipegosis					1	1	4	1		1		1																	
Wabigoon								1	1	1	1						1												
Otter		1	1			1				1				1															
Van Etten																1													
Portage								1																					
Kenogami					1																								
magnus																													
Lesser Slave														1				1	1	1	1								
hankinsoni																													
Oneida				2		1			1	2	3			1	1														
mendotae																													
Mendota									1					4	3	3	3		2	1		1							
Hammills														1															
woods																													
N Twin										1		2	1		1	2	3		3	2									
Whitestone														1			1												
Kawaguesaga									1	2	1	1	2	4	2	3	2	1	3	1	4		2						
Long															2	2				1	3								1
Shell															1														
Wolf												1					1												
Charter																		1		1									
manitoulinus																													
Typical form												1	1	3	1	2	4	1	4	2				1					

TABLE XVI

FREQUENCY DISTRIBUTION OF THE RATIO BETWEEN HEAD LENGTH AND MAXILLARY LENGTH (H/M) FOR SEVERAL DEEP-BODIED SUBSPECIES OF *Leucichthys artedi*

SUBSPECIES AND LAKE	25	26	27	28	29	30	31	32	33	34	35
tullibee											
Pine Island				2	2	2					
Winnipeg				1	6	4	1				
Lake of Woods		1	4	2	1						
Rainy			1								
Wakesiu				1	1		1				
winnipegensis											
Winnipegosis				3	1	3	2				
Wabigoon					1		3	1			
Otter					3	2					
Van Etten					1						
Portage					1						
Kenogami								1			
magnus											
Lesser Slave			1	1	1	1	1				
hankinsoni											
Oneida						3	5	1	1	1	
mendotae											
Mendota					2	4	3	7	1		1
Hammills							1				
woodi											
N Twin					3	7	2		2		
Whitestone						1	1				
Kawaguesaga			1		2	9	10	6			
Long						4	5				
Shell								1			
Wolf						1	1				
Charter					1		1				
manitoulinus											
Typical form	2	5	7	5							

TABLE XVII

FREQUENCY DISTRIBUTION OF THE RATIO BETWEEN PECTORAL LENGTH AND PECTORAL-VENTRAL DISTANCE (PV/P) FOR SEVERAL DEEP-BODIED SUBSPECIES OF *Leucichthys artedi*

SUBSPECIES AND LAKE	11	12	13	14	15	16	17	18	19	20	21
tullibee											
Pine Island				1		1	1				
Winnipeg			4	2	3	1	1				
Lake of Woods			2	1	3	1	2				
Rainy				1							
Wakesiu					2		1				
winnipegosis											
Winnipegosis		1		4	2	1					
Wabigoon			1	1	2		1				
Otter				2			1				
Van Etten						1					
Portage						1					
Kenogami					1						
magnus											
Lesser Slave	1		2	1	1						
hankinsoni											
Oneida					1	1	4	3		2	
mendotae											
Mendota					3	4	3	3	1		1
Hammills						1					
woodi											
N Twin				1	3	8	2		1		
Whitestone				1		1					
Kawaguesaga				1	7	7	10	3	1		
Long				3	1	1	3		1		
Shell					1						
Wolf		1			1						
Charter						1				1	
manitoulinus											
Typical form					1	9	7	2			

TABLE XVIII

FREQUENCY DISTRIBUTION OF THE NUMBER OF GILLRAKERS ON THE FIRST BRANCHIAL ARCH FOR THE RACES OF *Leucichthys artedi mackayi* AND THREE SIMILAR SUBSPECIES

SUBSPECIES	40	41	42	43	44	45	46	47	48	49	50	51	52	55
russelli														
Pine			1	6	8	5	5	2	1	3				
mackayi														
Stony					3	1	7	3	3			2		
Pigeon						1	1	1	3	4				
Granite						1	1	1	1	3				
Cameron					1	1	5	4	5	1				
Silver						1	1		2					
Sturgeon	1	1				3	3	1	1			1		
Upper Stony				1		3	1	1	1	1				
Garrison							1							
Kah-She						1	1							
Big Clam						1		1						
Sturgeon (Peterborough)					1	3	1		1	1	1			
Mill							1	1						
Balsam				1		1	2							
annensis														
Anne	1	3	3	5	6	10	7	3						
Bernard		1		1		1	1							
clarensis														
Clear					1	2	8	5	9	9	4	3	1	1

TABLE XIX

Frequency Distribution of the Ratio between the Length of the Body and Head (L/H) for the Races of *Leucichthys artedi mackayi* and Two Similar Subspecies

Subspecies	37	38	39	40	41	42	43	44	45	46	47
russeli											
Pine	1	7	9	10	3		1				
mackayi											
Stony			3	3	5	4	2				
Pigeon			1	3	1	1	4				
Granite			1	1	2	1					
Cameron				1	2	2	5	4	3		
Silver				3	1						
Sturgeon				1	1	4	2	2			
Upper Stony				1	3	4					
Garrison					1						
Kah-Sho					2						
Big Clam				1				1	1		
Sturgeon (Peterborough)				1	1	2	3	1			
Mill		1				1					
Balsam						1	1	2			
annensis											
Anne				1	1	1	4	9	15	7	3
Bernard						1		1	1	1	

Note — The specimens in this and the five succeeding tables are all under 200 mm., except those for Anne, most of which are under 225 mm.

TABLE XX

FREQUENCY DISTRIBUTION OF THE RATIO BETWEEN THE PECTORAL-VENTRAL DISTANCE AND THE PECTORAL LENGTH (PV/P) FOR THE RACES OF *Leucichthys artedi mackayi* AND TWO SIMILAR SUBSPECIES

SUBSPECIES	14	15	16	17	18	19	20	21	22
russelli									
Pine		4	13	10	4				
mackayi									
Stony	3	5	4	2	4	1			
Pigeon			3	4	2	1			
Granite			4	3					
Cameron	1			3	7	5		1	
Silver			2	1			1		
Sturgeon			1	2	3	4	1		
Upper Stony		1	2	2	2	1			
Garrison			1						
Kah-She		1							
Big Clam			1			2			
Sturgeon (Peterborough)				4	1		3		
Mill					1				
Balsam				1		2	1		
annensis									
Anne			2	3	4	7	9	2	2
Bernard				1	2		1		

TABLE XXI

Frequency Distribution of the Ratio between the Ventral-Anal Distance and the Length of the Ventral (AV/V) for the Races of *Leucichthys artedi mackayi* and Two Similar Subspecies

Subspecies	12	13	14	15	16	17	18	19
russelli								
Pine	1	6	13	12				
mackayi								
Stony		2	7	6	3	1		
Pigeon		1	5	1	3			
Granite		1	4		1			
Cameron				2	8	5	2	
Silver			1	2	1			
Sturgeon			2	5	2	1	1	
Upper Stony				4	3	1		
Garrison					1			
Kah-She			1	1				
Big Clam			1			1	1	
Sturgeon (Peterborough)				2	3		1	
Mill		1						
Balsam			1	1	1	1		
annensis								
Anne		1		2	7	10	7	1
Bernard			2		2			

TABLE XXII

Frequency Distribution of the Ratio between the Length of the Head and of the Snout (H/S) for the Races of *Leucichthys artedi mackayi* and Two Similar Subspecies

Subspecies	36	37	38	39	40	41	42	43	44	45
russeli										
Pine	1	4	13	7	3	2	1			
mackayi										
Stony		2	3	3	5	2	2	1		
Pigeon			3	2	4		1			
Granite			1		1					
Cameron			1	2	4	3				
Silver			1			2	1			
Sturgeon				4	3	1	2			
Upper Stony		1		1	3	1			1	
Garrison						1				
Kah-She						1			1	
Big Clam						1			1	1
Sturgeon (Peterborough)			1		3	3	1			
Mill			1				1			
Balsam			1	1	1	1				
annensis										
Anne		3	5	9	6	1	4	1		
Bernard			3							

TABLE XXIII

FREQUENCY DISTRIBUTION OF THE RATIO BETWEEN BODY LENGTH AND BODY DEPTH (L/D) FOR THE RACES OF *Leucichthys artedi mackayi* AND TWO SIMILAR SUBSPECIES

SUBSPECIES	4	4 1	4 2	4 3	4 4	4 5	4 6	4 7	4 8	4 9	5 0	5 1	5 2
russeli													
Pine	2	4	3	4	5	8	1	3					
mackayi													
Stony			1	1	4		2	2	2	1	2	1	
Pigeon					1		1	2		1	4	1	
Granite						1		4		1	1		
Cameron			1	2	2	2	3	1	2		2		
Silver		1	1				1						1
Sturgeon				1			1	1	2	2	1	1	
Upper Stony						1	2	1	1			1	
Garrison	1												
Kah She								2					
Big Clam	1		1		1								
Sturgeon (Peterborough)				1		1	2	1	1	1			
Mill							1						
Balsam							2	1		1			
annensis													
Anne	1	1	2	3	1	2	5	4	4	1		1	1
Bernard									1	1	2		

TABLE XXIV

FREQUENCY DISTRIBUTION OF THE NUMBER OF LATERAL LINE SCALES FOR TYPICAL *clarensis* AND THE *mackayi* RACES OF *L. artedi*

SUBSPECIES AND LAKE	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88
clarensis																						
Clear				1				1	1	1	1	7	6	4	7	6	4	3		2		1
mackayi																						
Stony				1		1	2	3	3	2	2	1	1	1				1		1		
Pigeon								1	2	4	3	2	3	3	2	2	3	1			2	1
Granite			1		2	3	2															
Cameron								1		1			2	1	4	4	2		1	1		
Silver							1	1	2													
Sturgeon					1					1			2		1	2		2	1	1		
Upper Stony									1		4	1				1		1				
Garrison					1																	
Kah-She								1		1												
Big Clam								1		1		1										
Sturgeon (Peterborough)									1	1		1	1			1	2					
Mill											1											
Balsam												1		1				1		1		

TABLE XXV

FREQUENCY DISTRIBUTION OF THE RATIO BETWEEN LENGTH OF HEAD AND MAXILLARY (H/M) FOR TYPICAL *clarensis* AND THE *mackayi* RACES OF *L. artedi*

SUBSPECIES AND LAKE	2.5	2.6	2.7	2.8	2.9	3.0	3.1	3.2	3.3	3.4	3.5
clarensis											
Clear				1	11	16	10	4	3		1
mackayi											
Stony		3	5	7	3						
Pigeon		1	3	5	1						
Granite				1		1					
Cameron			5	3	2						
Silver		1		3							
Sturgeon		1	4	4	1						
Upper Stony		1	2	3	1						
Garrison						1					
Kah-She			1		1						
Big Clam						1	1	1			
Sturgeon (Peterborough)			1	4	2	1					
Mill	1			1							
Balsam				2	2						

TABLE XXVI

Frequency Distribution of the Number of Gillrakers on the First Branchial Arch for Typical *L. a. artedi* and the Subspecies *clarensis clemensi* and *albus*

Subspecies	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55
artedi															
Michigan	1	2	7	18	24	46	57	62	49	37	44	22	14	4	4
Nichols					4	2	2	2	4	2					
Portage			1	2	2	1	7	7	6	3					
Walloon			1		2	1	2	2	5	1	1				
Hubbard				5	4	9	1	3	2						
Higgins					1	1	5	3	5	4	4	3			
Crystal		1	1	4	3	4	4	3	1						
Blind						1									
Elkhart							1	3	3	3	2				
Pine				1	1	1	6	6	7	6	3	1			
Champlain		1		2	1		1			1					
Beaver						1	1								
Sandy Bottom											1				
La Belle										1					
Little Trout								2	1						
Coldwater						1									
Cayuga							1			1					
Wolf								1	1						
Manitowik		1													
Otisco										1	1				
clarensis															
Clear				1	2	8	5	9	9	4	3	1			1
Allequash				2	1	2	4	6	5	2	1	1			
Palette				1	3	4	5	4	9	1	1	1			
Silver			1	3	4	5	5	1	2					2	
Stormy					1	4	3	7	5	6	1	2		1	
Muskellunge			1	4	4	7	13	2	4	4	2		1		
Okauchee							1		3						
Mamie													2		
Pine						1	2	2		2	1				
Dead Pike						1									
Orchard					1		1		1						
Whitewood					1					1	1				

TABLE XXVI (*continued*)

SUBSPECIES	41	42	43	44	45	46	47	48	49	50	51	52	53	54
clarensis														
Ore						1		2	1					
Marble						1		1						
Sand		1												
Round				1			3	2	1					
Douglas					5	2	6	21	14	14	9	4		1
Burt				2	2	1	7	8	7	5				
Fowler											1			
Fence			2	1	3	3	5	4	4	1				
clemensi														
Nipigon	1	1		2	4	10	14	11	14	5	6	2	1	
Fanny Hoe						1		5	2					
Gulliver							1							
Mountain		2	6	18	19	32	21	8	7	2				
Ives				4	17	30	19	28	17	8	1			
Trout						2	5	2	1	1			2	
albus														
Erie	2	5	23	32	37	56	58	40	41	13	3		1	2
Mindemoya			2		2	2	3	2	1					

TABLE XXVII

FREQUENCY DISTRIBUTION OF THE NUMBER OF LATERAL LINE SCALES FOR *L. a. artedi* AND THE SUBSPECIES *clarensis clemensi albus sisco* AND *lowei*

SUBSPECIES	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94
artedi																											
Michigan	1			1	1	3	2	6	13	15	15	19	24	40	37	38	29	40	24	20	13	14	5	4	2	4	1
Nichols													1		1	1		2	1	3	3	1	2		1		
Portage										1	1	2	2	2	4	2	2	8	4	3		1			2		
Walloon											1	1	3	6	2	1	2	2	7	3	3						
Hubbard									2	1	2	2	2	4		3	5	1	1	1	2						
Higgins													1		1	1		2	1	3	3	1	2		1		
Crystal				1	1				1	1		3	3	4		4	1	1									
Blind																											1
Elkhart								3		2		4	2		1				1								
Pine									2	1	1	2	4	2	2	2	4	3	1	2	2		2			1	1
Champlain			1		1				2					2				1			1						
Beaver														1	1												
Sandy Bottom																		1									
La Belle																		1									
Little Trout												1	1						1								
Coldwater																								1			
Cayuga													2														
Wolf																					1						
Manitowik								1																			
Otisco												1						1									

TABLE XXVII (*continued*)

SUBSPECIES	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92
clarensis																												
Clear							1			1	1	1	1	7	6	4	7	6	4	3		2		1				
Allequash								1		2	1	2	2	2	3	5		2	1	1								
Palette											1	3	4	3	3	1	2	2	3		1	1	2	1	1			
Silver							1	1			1	3	5	4	2	1	1	2	3									
Stormy								1	0	0	1	0	4	2	3	5	4	3	2	2	1	1	1					
Muskellunge							1	1		2	1		4	5	1	4	10	4	3	2	1	1	1	1				
Okauchee															1	1		1						1				
Mamie									1								1											
Pine																		1	1	1			3		1			1
Dead Pike																					1							
Orchard																			1	1	1							
Whitewood																		1			1			1				
Ore															2	1						1						
Marble																		1							1			
Sand																			1									
Round				1			1	1		1		2	1	1														
Douglas	1		1		2	1	1	4	5	5	8	6	9	9	8	3	6	2	4	3	1	2						
Burt						1	2		4	3	2	3	6		6		2		3									
Fowler																1												
Fence						1	1	1	1	1	3	2	2	1	2	2	1	2		1								
clemensi																												
Nipigon	1			3	4	5	9	7	6	10	6	8	3	4	3	2	1											
Fanny Hoe							2		2	1							2		2									

TABLE XXVII (*concluded*)

Frequency Distribution of the Number of Lateral Line Scales for *L. a. artedi* and the Subspecies *clarensis* *clemensi*, *albus* *sisco* and *lowei*

Subspecies	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94
clemensi																															
Gulliver															1																
Mountain				1	1	1	6	3	5	4	8	16	18	17	16	5	3	4	2			1									
Ives				1	1		3	1	2	9	16	8	11	13	14	13	13	7	7	6	1	1									
Trout						1	1	2	1	2		2	1	2	1	1															
albus																															
Erie	1		2	3	6	17	22	35	48	64	80	76	97	74	66	47	35	31	14	12	9	7	2		1	1					
Mindemoya		1	1				3	2	3			1			1																
sisco																															
Corey										1	1		1	2	4	2	8		1	3	1					1					
Klinger																							1		1		2	1			1
Murry																					1										
Harwood										1		1		1			1	1													
Oconomowoc																	1		1	2		1	2	1		1					
Island																	2				1							1			
Geneva								1		1	1	3	2	5	3	9	18	13	11	13	12	9	3	3		4	1				
Gordy																				1		1	1	1							
Indian Village																	1	1				1									
Pine																				1											
Tippecanoe																						1			1						
Hulbert										1		1	4	5	3	6	11	8	4	8	8	1	4	3			2	1	1		
Black Oak									1			3	1	1	4	4	1	1	1	4	2	2	3		1		2				

TABLE XXVIII

FREQUENCY DISTRIBUTION OF RATIO BETWEEN HEAD LENGTH AND SNOUT LENGTH (H/S) FOR TYPICAL *L artedi artedi* AND *L a clarensis*

SUBSPECIES AND LAKE	3 3	3 4	3 5	3 6	3 7	3 8	3 9	4 0	4 1	4 2	4 3	4 4	4 5	4 6
artedi														
Michigan *	2		3	16	24	30	19	26	5	5	1	1		
do		2	8	24	40	36	20	12	2					
clarensis														
Clear					1	7	6	12	8	4	5	2		
Allequash						1	8	7	6	8	2	2		
Palette						1	4	7	7	6	1	1		
Silver					3	6	7	6	2					
Stormy				1		1	1	4	6	12	4	1		
Muskellunge				1	3	1	5	10	11	9	2	1		
Okauchee							1	1	2					
Mamie						1				1				
Pine						1		2	2	2	1			
Dead Pike										1				
Orchard *								2		1				
Whitewood								1	1			1		
Ore *						1		1	1	1				
Marble								1		1				
Sand														1
Round							1	4	2			1		
Douglas				3	1	8	10	19	13	15	8	2	1	
Burt					2	2	6	9	3	8		1	1	
Fowler *										1				
Fence							4	6	3	2	1	2	1	1

* These fish are over 225 mm long except one specimen from Ore Lake, most of the others are under that limit

TABLE XXIX

Frequency Distribution of Ratio between Length of Head and Maxillary (H/M) for Typical *L. artedi artedi* and *L. a. clarensis*

Subspecies and Lake	2 4	2 5	2 6	2 7	2 8	2 9	3 0	3 1	3 2	3 3	3 4	3 5	3 6
artedi													
Michigan *		5	7	21	37	36	21	3	2	1			
	1	3	16	39	44	23	17	2					
clarensis													
Clear					1	11	16	10	4	3		1	
Allequash				2	5	2	11	4					
Palette					1	7	11	5	3	1			
Silver					2	9	8	5					
Stormy					1	6	10	9	4				
Muskellunge				1	5	9	18	8	2				
Okauchee							4						
Mamie					1		1						
Pine						1	2	2	2		1		
Dead Pike					1								
Orchard *								1	1	1			
Whitewood						1	1	1					
Ore *							1	1	1				1
Marble								1		1			
Sand										1			
Round						2	4	1	1				
Douglas			1	6	35	23	13	3					
Burt					7	16	6	3					
Fowler *									1				
Fence			1		3	10	6		1	1			

* *See note to Table XXXVIII*

TABLE XXX

DISTRIBUTION OF RATIO BETWEEN BODY LENGTH AND HEAD LENGTH (L/H) FOR TYPICAL *L. artedi artedi*, *L. a. sisco* AND *L. a. clarensis*

SUBSPECIES AND LAKE	3 6	3 7	3 8	3 9	4 0	4 1	4 2	4 3	4 4	4 5	4 6	4 7	4 8	4 9	5 0
artedi															
Michigan					5	14	30	36	32	21	8				
sisco															
Geneva							4	12	25	33	24	11	3	1	
clarensis															
Clear					2	7	11	11	4	3	3	1			
Allequash				3	1	7	11	3							
Palette							5	3	6	6	4	1	2		
Silver							1	5	6	8	2	2			
Stormy						1	5	6	9	5	4				
Muskellunge						2	7	15	11	7					
Okauchee								1		2	1				
Mamie							1				1				
Pine					2	3	1	2							
Dead Pike						1									
Orchard *							1	1	1						
Whitewood					1	1	1								
Ore *						2		2							
Marble					1	1									
Sand									1						
Round							1	6	1						
Douglas	1	4	5	23	24	13	11								
Burt				1	1	7	10	8	5						
Fowler *												1			
Fence				1	5	8	4	3	1						

* These fish are over 225 mm. long, except one specimen from Ore Lake, most of the others are under that limit

TABLE XXXI

Frequency Distribution of Ratio between Pectoral Length and Pectoral-Ventral Distance (PV/P) for Typical *L artedi artedi*, *L a. sisco* and *L a*

Subspecies and Lake	1 4	1 5	1 6	1 7	1 8	1 9	2 0	2 1	2 2	2 3	2 4	2 5	2 6
artedi													
Michigan			3	5	20	23	57	21	10	1		1	
sisco													
Geneva				1	3	14	28	26	23	14	2		1
clarensis													
Clear		3	7	14	7	5	4	1	2	1			
Allequash			6	10	4	2	1						
Palette			2	7	5	8	5						
Silver			2	2	5	8	3	2					
Stormy		1	1	5	8	7	5	2					
Muskellunge		2		4	15	15	7						
Okauchee						1	2	1					
Mamie			1			1							
Pine			1	1	2	2	2						
Dead Pike					1								
Orchard *						1	1				1		
Whitewood			1	1	1								
Ore *				1	1	2							
Marble					2								
Sand							1						
Round				1	2	5							
Douglas	1	8	18	22	24	8	2						
Burt			1	2	12	9	8						
Fowler *									1				
Fence			3	6	5	6	1	1					

* These fish are over 225 mm long, except one specimen from Ore Lake, most of the others are under that limit

TABLE XXXII

FREQUENCY DISTRIBUTION OF THE NUMBER OF GILL RAKERS ON THE FIRST BRANCHIAL ARCH FOR TYPICAL *L. artedi* AND THE TWO SUBSPECIES *microcephalus* AND *sisco*

SUBSPECIES AND LAKE	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55
artedi															
Michigan	1	2	7	18	24	46	57	62	49	37	44	22	14	4	4
microcephalus															
Gogebic				3	2	1	1	2	1						
sisco															
Corey			2	1	4	3	8	3	1	1	2				
Klinger			1			2	2	1							
Murry								1							
Harwood					2	1	2								
Oconomowoc								3	0	3	2	1			
Island						2	2								
Geneva		3		4	13	27	28	12	9	5	4	2	1		
Gordy					1		2		1						
Indian Village								1			1				
James									1						
Tippecanoe					1	1									

TABLE XXXIII

Frequency Distribution of the Ratio between Body Length and Head Length (L/H) for Typical *L. artedi* and the Subspecies *microcephalus* and *sisco*

Subspecies and Lake	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57
artedi																		
Michigan − 225 mm	5	14	30	36	32	21	8											
Michigan + 270 mm			4	3	5	7	5	4	2		2							
microcephalus																		
Gogebic + 213 mm											2	3	1	2				1
sisco																		
Corev + 270 mm						1	2	4	5	7	3	2						
Klinger + 300 mm						1	1	3		1								
Murry 200 mm							1											
Harwood + 240 mm					1	1				1	2							
Oconomowoc − 272 mm						1	5	2	1	1								
Island − 200 mm						1	1	1	1									
Geneva − 225 mm			4	12	25	33	24	10	3	1								
Gordy + 270 mm								1	1	2								
Indian Village + 270 mm		1				1		1										
James 208 mm.					1													
Tippecanoe 157 169 mm				2														

TABLE XXXIV

FREQUENCY DISTRIBUTION OF THE RATIO BETWEEN HEAD LENGTH AND SNOUT LENGTH (H/S) FOR TYPICAL *L. artedi* AND THE SUBSPECIES *microcephalus* AND *sisco*

SUBSPECIES AND LAKE	3 4	3 5	3 6	3 7	3 8	3 9	4 0	4 1	4 2	4 3	4 4	4 5	4 6	4 7
artedi														
Michigan { − 225 mm	2	8	24	40	36	20	12	2						
Michigan { + 270 mm		1	2		9	4	7		2					
microcephalus														
Gogebic							2		3	1			1	
sisco														
Corey					1	4	7	4	3	4		1		
Klinger								2	1	2		1		
Murry										1				
Harwood							1	2						
Oconomowoc					2	1	1	3	2			1		
Island				1	1		1		1					
Geneva		2	3	7	15	10	46	9	11	1	2			
Gordy					2		1							1
Indian Village				1	1		1							
James						1								
Tippecanoe							1		1					

TABLE XXXV

FREQUENCY DISTRIBUTION OF THE RATIO BETWEEN HEAD LENGTH AND MAXILLARY (H/M) FOR TYPICAL *L. artedi* AND THE SUBSPECIES *lus* AND *sisco*

SUBSPECIES AND LAKE	2 4	2 5	2 6	2 7	2 8	2 9	3 0	3 1	3 2	3 3	3 4	3 5	3 6
artedi													
Michigan { − 225 mm	1	2	16	39	44	23	12	2					
Michigan { + 270 mm				5	9	12	6		1				
microcephalus													
Gogebic							2	3	3	1			
sisco													
Corey						4	8	6	6				
Klinger								2	1	1	1		1
Murry								1					
Harwood						1	2	1	1				
Oconomowoc						2	4	2	1	1			
Island						2	0	2					
Geneva			1	3	18	45	26	13	5				
Gordy								1	1	2			
Indian Village							1	1	1				
James						1							
Tippecanoe					1		1						

TABLE XXXVI

Distribution of the Ratio between Ventral Length and Ventral-Anal Distance (AV/V) for Typical *L artedi* and the Subspecies *microcephalus* and *sisco*

Subspecies and Lake		13	14	15	16	17	18	19	20	21	22	23
artedi												
Michigan	− 225 mm	2	7	27	50	37	11	5	1			
	+ 270 mm				2	6	9	7	3		2	1
microcephalus												
Gogebic						1	1	1	1	3		1
sisco												
Corey						1	6	10	6	1		1
Klinger							2		4			
Murry						1						
Harwood					1		3	1				
Oconomowoc					3	2	2	2	1			
Island					2		1	1				
Geneva				12	36	40	20	3	2			
Gordy					2	1		1				
Indian Village					1				2			
James				1								
Tippecanoe				1	1							

TABLE XXXVII

Frequency Distribution of the Ratio between Pectoral Length and Pectoral-Ventral Distance (PV/P) for Typical *L artedi* and the Subspecies *microcephalus* and *sisco*

Subspecies and Lake	17	18	19	20	21	22	23	24	25	26	27
microcephalus											
Gogebic					6		2		1	1	
sisco											
Corey					5	8	11	1			
Klinger			1	1	1	3					
Murry				1							
Harwood			2	2		1					
Oconomowoc			3	2	2	2					1
Island	1		2		1						
Geneva	1	3	14	28	26	23	14	2	1		
Indian Village	1				1	1					
Gordy			1			1	1	1			
James			1								
Tippecanoe			1	1							

TABLE XXXVIII

Frequency Distribution of the Number of Gillrakers on the First Branchial Arch for the Various Races of *Coregonus clupeaformis*

Subspecies and Lake	22	23	24	25	26	27	28	29	30	31	32	33
clupeaformis												
Michigan			1	9	44	43	42	11	1			
Torch					[illegible]	5	2	2				
latus												
Erie				3	18	21	36	20	2			
Walnut		1		1	1	5	9		2			
neo-hantoniensis												
Winnepesaukee					1							
Otsego						1	5	3				
Beau						1	1		1			
Glacier				1			1					
Umsaskis					2							
Champlain					1							
Chazy					1							
Kiwassa					2	1						
Clear				1	1							
Eagle				1								
Upper Saranac			1	2	1	1	1	1				
Lower Saranac				1								
Simcoe			1	1	1							
Mindemoya					1	1						
Upper St. Mary's				2	1	2	1					
Siskowit				13	8	4						
Stone					4	8	4	3	1			
Athabaska				2	2	1						
Granite					1		3					
Upper Stony			1		1							
Thames			1	2	3	1	1					
gulliveri												
Gulliver										1	3	1
Allegash											1	
Chateaugay										2	2	
Sturgeon												1
Chicogan												1
dustini												
Desor				1	6	13	29	26	24			
Trout			1	1	12	26	10	3				
medorae												
Medora							5	5	3	8	1	1
stanleyi												
Cross Lake	1			3	15	2						
Penobscot					1	1						
Telos				1		1						
Eagle						1						
Square				1	1							

TABLE XXXIX

Frequency Distribution of the Number of Lateral Line Scales for the Various Races of *Coregonus clupeaformis*

Subspecies and Lake	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93
clupeaformis																								
Michigan					1	1	1	3	2	7	7	17	12	17	16	23	29	18	14	9	5	5	2	2
Torch											1	2	1	1	3	1	1	1					1	
latus																								
Erie				2	3	8	6	18	19	24	44	44	35	30	25	16	15	13	6	5	6	3		1
Walnut										2	1	3	3	2	2	2	1		2	1				
neo-hantoniensis																								
Winnepesaukee																1								
Otsego									1			1		1	1	1	1	1			1	1		
Beau									1			1			1									
Glasier								1								1								
Umsaskis	1			1																				
Champlain			1																					
Chasy												1												
Kiwassa										1	2													
Clear								1			1													
Eagle												1												
Upper Saranac						1				1		1	2	1			1							
Lower Saranac														1										
Simcoe													1	1					1					
Mindemoya								1							1									

TABLE XXXIX (*continued*)

FREQUENCY DISTRIBUTION OF THE NUMBER OF LATERAL LINE SCALES FOR THE VARIOUS RACES OF *Coregonus clupeaformis*

SUBSPECIES AND LAKE	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97
Upper St. Mary's															1			2		2		1								
Siskowit											2	2	3	4	4	2	1	1	1		1	1								
Stone										1	4	4	4	1	2	2	4		1											
Wabigoon														1																
Athabaska								1	1	1					1															
Granite																		1		1		2								
Upper Stony																1														
Thames							1		1	1		1	1		2		1			1										
gulliveri																														
Gulliver									1					2		1														
Allegash									1																					
Chateaugay	1					3			1	1	2																			
Sturgeon																		1												
Chicogan													1																	
dustini																														
Desor																	3	4	3	7	10	7	5	9	11	10	4	3	2	1
Trout									1	1	1	2	2	4	2	9	5	9	5	2	2	3	2	1	1					
medorae																														
Medora											2	4	1	2	1	2	2	3	2	2	2					1				
stanleyi																														
Cross								2	1	2	4	5	2	3	2	2	1													
Penobscot						1						1				1														
Telos										1						1														
Eagle																					1									
Square															1										1					

TABLE XL

Frequency Distribution of the Ratio of the Pectoral Length and the Pectoral-Ventral Distance (PV/P) for the Various Forms of *Coregonus clupeaformis*

Subspecies and Lake	12	13	14	15	16	17	18	19	20	21	22
clupeaformis											
Michigan – 250 mm					5	5	7	8	11	4	2
Torch						3	3	6			
latus											
Erie					1	3	4	9	1		
Walnut		1		2	4	5	5		1	1	
neo-hantoniensis											
Winnepesaukee					1						
Otsego	1	1	1	3	2	1					
Beau		1		1	1						
Glamer		1				1					
Umsaskis	1			1							
Champlain					1						
Chazy		1									
Kiwassa			1	1	1						
Clear				2							
Eagle							1				
Upper Saranac		1		2	4						
Lower Saranac				1							
Simcoe					2	1					
Upper St Mary's			1	4	1						
Siskowit		1		7	8	2	3	2		1	
Stone	1	5	5	6	3						
Wabigoon		1									
Athabasca			2		1	1					
Granite		1	1	1		1					
Upper Stony			1		1						
Thames		2	2	3	1						
gulliveri											
Gulliver		1	2		1						
Allegash			1								
Chateaugay	1	1	3	2		1					
Sturgeon						1					
Chicogan			1								
dustini											
Desor			2	8	7	1	4	1			
Trout	3	9	12	10	8	6	2	3			
medorae											
Modora			1	5	7	6	4				
stanleyi											
Cross		2	12	7	2	1					
Penobscot						2	1				
Telos		1	1								
Eagle		1									
Square			1	1							

TABLE XLI

Frequency Distribution of the Ratio between Body Length and Head Length for the Type Races of the Various Subspecies of *Coregonus*

Subspecies	3 7	3 8	3 9	4	4 1	4 2	4 3	4 4	4 5	4 6	4 7	4 8	5 1
stanleyi – 205 mm							1	1	4	5	7	3	
clupeaformis – 300 mm						2	5	12	10	10	9	14	
latus + 300 mm											5	5	
neo-hantoniensis 240 mm										1			
medorae – 275 mm									1			6	
dustini – 300 mm	1		1	4	4	7	5	1					
gulliveri 218–395 mm										3		1	

TABLE XLII

Frequency Distribution of the Ratio between the Length of the Body and the Length of the Head (L/H) in Races of *Prosopium quadrilaterale*

Lake	4 5	4 6	4 7	4 8	4 9	5	5 1	5 2	5 3	5 4	5 5	5 6
Michigan + 200 mm					1	4	5	5	7	7	4	1
Michigan – 200 mm			2	4	3	20	8	2				
Mirror + 200 mm						1						
Clear Pond + 200 mm					1		1					
Big Clear + 200 mm						1						
"Adirondacks" + 200 mm				2			1					
Cross + 200 mm			2	3	3	1						
Umsaskis – 218 mm	1			1								
Village + 200 mm										1		
Newfound + 200 mm								1				
Chazy – 215 mm		2	7	7	3							

TABLE XLIII

Frequency Distribution of the Ratio between the Ventral-Anal Distance and the Ventral Length (AV/V) in the Races of *Prosopium quadrilaterale*

Lake	1.6	1.8	1.9	2.0	2.1	2.2	2.3	2.4	2.5
Michigan*					6	7	12	2	1
do					13	12	3		
Mirror							1		
Clear Pond						2			
Big Clear					1				
"Adirondacks				1	2				
Cross	1		1	6	1	1			
Umsaskis				1	1				
Village								1	
Newfound				1					
Chazy			3	11	5		1		

* For size of specimens see Table XLII

TABLE XLIV

Frequency Distribution of the Ratio between the Pectoral-Ventral Distance and Pectoral Length (PV/P) in the Races of *Prosopium quadrilaterale*

Lake	1.4	1.5	1.6	1.7	1.8	1.9	2.0	2.1	2.2	2.3
Michigan *					1	4	7	10	3	1
do					6	17	15	4		
Mirror			1	1						
Clear Pond					1					
Big Clear					1					
"Adirondacks	1			1	1					
Cross			2	2	5	1				
Umsaskis				2						
Village						1				
Newfound					1					
Chazy		3	8	5	4					

* For size of specimens see Table XLII

TABLE XLV

FREQUENCY DISTRIBUTION OF THE NUMBER OF LATERAL LINE SCALES IN RACES OF *Prosopium quadrilaterale*

LAKE	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100
Michigan						1	1		4	6	8	5	4	10	6	3	6	4	2	2	2	1
Mirror										1												
Clear Pond						1		1														
Big Clear									1													
' Adirondacks								1			1					1						
Cross			1				3	1	2	1	2											
Umsaskis										1		1										
Village															1							
Newfound																				1		
Chazy	2		7	3		1	2	3		1		1										

TABLE XLVI

FREQUENCY DISTRIBUTION OF THE NUMBER OF GILLRAKERS ON THE FIRST BRANCHIAL ARCH IN RACES OF *Prosopium quadrilaterale*

LAKE	14	15	16	17	18	19
Michigan		4	5	10	6	1
Mirror				1		
Clear Pond					2	
Big Clear				1		
"Adirondacks			2	1		
Cross				5	4	1
Umsaskis				2		
Village			1			
Newfound						1
Chazy	1	8	7	3	1	

OBSERVATIONS ON THE LIFE-HISTORY OF *RHEUMATOBATES RILEYI* (BERG.) (HEMIPTERA-GERRIDAE)*

J. K. GWYNN SILVEY

SOME knowledge of the oviposition and nymphal instars of the crooked-legged water-strider, *Rheumatobates rileyi*, has been desired since the discovery of the species in July, 1890. It is the intention of the writer to describe certain features of the biology and the general life-history of this peculiar bug. The Michigan form has been described as *R. rileyi* var. *palosi* by Blatchley.

This work was done under the direction of Professor H. B. Hungerford, at the University of Michigan Biological Station during the summers of 1927 and 1928. The author also wishes to express indebtedness to Professor George R. La Rue, for use of the facilities at the Biological Station, and to Professor Paul S. Welch, for aid and helpful suggestions.

Rheumatobates rileyi was described by Bergroth (1891) from one specimen collected on Long Island, New York. Riley and Howard (1891) gave a description and figure of the male of this species. Heidemann (1893) collected many specimens from the Potomac Canal near Washington and sent them to Riley. Riley and Heidemann attempted to show a normal and an abnormal type of male in this species and gave an account of the sexual dimorphism. There was included a description of the nymphal forms of both the "abnormal" and the normal males. According to Heidemann, the striders are able to dive under the surface of the water when someone approaches. They are very shy creatures. Bergroth (1908) showed that the forms described by Riley and Heidemann as "abnormal" are really the true *R. rileyi*, and the ones that he thought to be normal were *R tenuipes* He also includes the statement that members of this species are able to live only on running water and that therefore it would be a difficult task to culture them in the laboratory Hungerford (1919) states "that three summers have failed to disclose the nature of the oviposition " He also describes some very interesting food habits which the writer has been able to verify

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* Contribution from the Biological Station and the Zoölogical Laboratory of the University of Michigan.

GENERAL STATEMENTS

The male of *R rileyi* (Fig 1) is very much different from the female of this species Among the Hemiptera one is unable to find a genus of bugs that shows more variations from the normal form The clasping antennae, the peculiar twist of the hind femora, and the attachment of the hind tibia apart from the apical end of the femur are all points of differentiation A peculiar characteristic of this species is the great curvature of the hind femora When they are at rest they will form almost a true circle, so great is the curvature

The female of *R rileyi* (Fig 2) does not show so many bizarre shapes The antennae resemble those of the other gerrids, the hind femora are neither twisted nor curved, and the tibiae are attached directly to the apical end of the femora Thus, the sexual dimorphism of the species is as well demonstrated here as in any other members of the order Hemiptera In addition, the female possesses a sword-shaped ovipositor

METHODS

COLLECTING APPARATUS

The ordinary dip-net was far too coarse to be used in collecting these water-striders and the regular collecting net was not serviceable because it would destroy the specimens by the force of the water going through the mesh A large-size milk strainer was secured and the top covered with a fine-meshed bolting cloth that was drawn taut A handle was attached to the net so that it could be manipulated accurately and swiftly Two buckets were provided, one smaller than the other, so that the larger might be partially filled with water and the smaller supported in it In this manner the vibration of the motor boat would not too greatly disturb the insects while they were being transported to the laboratory The collector, in order to get as close as possible to the surface of the water and not disturb the striders, had to sit on the edge of the boat and collect in a very deliberate manner After a number of specimens were caught in the net, it was inverted over the smaller bucket, which was partially filled with water, and the insects were shaken out upon the surface of the water Some of the bugs would break through the surface film because the force with which they were thrown into the bucket was too great, and these would have a difficult time getting back again to the surface It was noted many times, however, that, if they were under the surface at the beginning of the trip from the place of collection, they would be on the surface by the time they reached the rearing jars This was due possibly to the continual breaks in the surface film produced by the vibration of the outboard motor, which permitted the insects to gain the surface

The shaded aquarium building and the sunny insectary were used as shelters for the rearing jars Several containers partially filled with water were used, the size varying from that of the finger-bowls to the larger battery-jars Only one pair of specimens was placed in the smaller containers, while in the larger ones many were reared

HABITAT AND DISTRIBUTION

The only specimens of *R rileyi* collected in the region of Douglas Lake were found on Bessey Creek, about two hundred feet from its entrance into the lake and thence onward upstream for about one fourth of a mile They were never found on the rapidly running parts of the creek, but only on the very slow running areas The shore-line in this particular part of the creek was covered with sweet gale (*Myrica gale*), the branches of which bent over so that a large part of the foliage was in direct contact with the water In addition, there were many water-lilies (*Nym-*

phasa and *Castalia*), and an abundance of *Potamogeton* The creek was filled with old logs and many kinds of débris which made passage of a boat difficult Larger trees bordered the shore-line for the entire length of the creek so that the water was shaded during the larger part of the day

On Bessey Creek, the water-striders seemed always to prefer the more protected parts where the water was running very slowly, and where there was an abundance of submerged or emergent vegetation They were seldom found on the sunny part of the water surface, but rather in the shaded portion If ostracods or partially drowned small insects were present on or near the surface, the bugs would congregate there From notes of previous workers it seems that this species may and often does prefer the swiftly running streams According to the writer's observations, it is rather difficult for this species to survive on such water, since almost any ripple will put these bugs under the surface

LABORATORY CULTURE

Containers in which the nymphs and adults were raised have already been described in another section of this paper The water in these containers, although varying in depth with the type of receptacle used, was changed daily in some of them and by continuous stream in others With each change in water, the particles that had collected on the surface were removed, so that they would not hinder the striders in their movements The rearing jars were always kept covered with several thicknesses of fine cheesecloth to prevent the entrance of most kinds of débris, or to retain any winged forms which might emerge The water was changed more frequently in the insectary rearing jars which were placed in direct sunlight, than in those in the aquarium building, since they were more exposed Two of the larger insectary containers had a continuous water supply from a large reservoir which was kept full of unmodified lake water

The insects in the rearing jars were fed daily on a variety of the smaller insects taken in the sweepings around the Biological Station Those insects remaining uneaten were removed on the following day, when the water was changed, so that conditions remained fairly constant Occasionally, as the chance presented itself, a number of ostracods were introduced into the jars, and these were generally eaten immediately

BIOLOGY

GENERAL FOOD HABITS

R rileyi is not a very discriminating insect as regards food, provided it can be eaten easily and rapidly In a habitat containing many ostracods, this bug has been seen to scoop up one and run around on the surface of the water with the small prey on the end of the upturned beak Likewise, if any of the smaller insects, especially Diptera and Homoptera, fall into the water, the bugs will immediately pierce them with the beak, raise them on the end of it, and run around continually until all of the usable material is removed from the body, after which it is cast aside If striders are smaller than the insect that is to serve as prey, several will congregate about it, and will soon devour all the available nourishment They have not been observed by the writer feeding on any animals larger than insects or smaller than some of the ostracods They feed entirely on animals and are generally predacious, although they will become scavengers when deprived of food for a long time They have been known to feed on dead members of their own species

PREDATORY HABITS

These bugs frequently attack insects that are alive and have just fallen into the water At such times they kill the prey by piercing it with the beak and throwing it up above the head, so that it can struggle very little If the insect that they wish to prey upon is larger and more powerful than they are, they pierce it many times, then proceed to feed at once Often the striders will enter into struggles with other insects and the writer has observed the would-be predator killed and the intended prey escape This is, however, very rare and has been observed only twice, once in a combat with a small wasp (*Evaniidae*), and, the other time, with a fly that escaped before it was collected Cannibalism has not been observed in this species, nor has fighting been seen within the group

NOCTURNAL LIFE

Although closely packed together on the surface of the water, the striders feed more actively during the night than the day Likewise, mating is essentially a nocturnal phenomenon both in the rearing jars and in the field However, so far as observed, locomotion activity differed little during day or night Striders in the act of mating were disturbed by a weak artificial light to such a degree that many of them would part as soon as the light fell on them Such light also caused many to cease feeding

BREEDING HABITS

R rileyi is so very shy that observations of the mating are difficult There was available to the writer a large number of specimens, which made possible repeated observations on the mating Generally, as has been noted above, this takes place at night, that is, just after twilight However, it has been observed during the day in the rearing jars as well as in the natural habitat

The peculiarly shaped antennae of the male are very useful in the mating process In copulation they are curved in such a way that the base of the first segment lies just above the first antennal segment of the female Near the distal end of the first segment the antennae of both female and male are almost parallel The third segment of the antennae of the female is placed above the third segment of the male and in this manner passes over at the disk-like organ on each antenna of the male In some instances the antennae of the female pass directly over the disk-like organ, at other times, it passes on either side of it Immediately behind the dorsal placement of the female antennae, there is a bend in the joint between the last two segments, so that the fourth segment extends again below to the male antennae and is twisted, so that it is caught in the subapical spur on the fourth segment In this manner the clasping of the female antennae by the male is so complete that there is little doubt that this strange antennal structure is an adaptation for mating

In mating, the mesothoracic legs of the male are lifted clear of the water and are held in a horizontal position at right angles to the body The female generally makes use of the mesothoracic legs as organs of locomotion, since there is no cessation of movement during mating The metathoracic legs of the male are curved around those of the female The curvature of the femora of the male encircles those of the female and the tarsi of both touch the water and perform their usual task in locomotion

Additional features of mating do not differ essentially from those of the other gerrids, so that there is little use in describing them in this paper

EGG-LAYING HABITS

The writer has observed one female in the act of oviposition It was resting on a floating Potamogeton leaf, with the ovipositor inserted in the tissue just at the base of the leaf Examination of the stem of the plant revealed five eggs placed centrally in the interior, with very indistinct punctures in the epidermis of the plant showing where the ovipositor had entered These punctures were a little more than a millimeter apart on the same side of the stem

After the method of oviposition had been discovered, a large quantity of Potamogeton was collected and examined for eggs Four groups of eggs were found, varying in number from three to nine in the various stems

The writer is unable to state whether the striders make use of other sorts of material or not, and the number of egg groups found is too small to permit any conclusion as to the regular number deposited at one time It is hoped that more complete data will be secured during the coming summer (1930)

GENERAL HABITS

In all the instars, these insects are both very gregarious and shy Apparently, the first and second instar nymphs exhibit these characteristics much more than do any of the older forms. All the striders, from the third instar to the adult, move smoothly on the surface of the water, the first and second instars hopping along rather than moving evenly A collecting net drawn over the surface of water supporting a large population of very young bugs secures many individuals because in this stage they are less active and more aggregated This collecting method becomes less effective with increasing instars, owing to the greater activity of the animals, so that very few adults are collected with ease

On damp cool days the insects congregate near the bank of the stream, many times under the overhanging sweet gale or branches of willow which dip down into the water On warm days they may be found in the center of the stream, where the shade is less dense, but generally not in the sunshine They are seldom at rest, generally moving continually over the surface of the water in search of food If they are disturbed, they will move very swiftly and seek some sheltered corner or nook, after which they are very hard to find and collect

R rileyi is gregarious not only with members of its own species, but also with those of different genera and species It is not at all uncommon to see individuals of *Gerris* and *Trepobates* mixed in a group of *Rheumatobates* It has been stated in the literature that different species of this genus will many times be found with *R rileyi*, which explains the confusion that has arisen in the species of this group On Bessey Creek there was only one species of *Rheumatobates*, so that the writer could not verify these records In Dallas County, Texas, the writer frequently observed two species of this genus, viz , *R hungerfordi* and *R tenuipes*, in the same group

LIFE-HISTORY

The entire life-history of *R rileyi* was worked out in two different ways and both checked in all details The first method was that of rearing the instars as they were brought in from day to day and preserving some from each of the stages At the end of the series five different instars had been raised in the rearing jars In the second method, collections made daily from the creek yielded a series of specimens representing the successive instars as developed in nature The results of the two methods agreed in all details Eggs collected from plants in the field and fully developed eggs dissected from females hatched in due time, thus providing the first nymphal instar The stadia were all about eight days long

EGG

Whitish-gray, elongate, cylindrical, with one end slightly pointed to blunt, opposite end flattened to round, bearing one short projecting micropyle (Fig 8)

Size — Length 0 680 0 740 mm , width 0 190 0 220 mm (preserved material)

FIRST INSTAR

Size — Length of body 0 837-0 953 mm Width of head, including eyes, 0 442–465 mm (preserved material) (See Fig 7)

Shape — Flattened, width of mesothorax two thirds of length of body Length of prothorax one half that of abdomen Width of head, including eyes, equal to width of abdomen at second proximal segment General form of body subovate with distinct indentation between meso- and metanotum

Color — Head Y-shaped suture, ventral margins and central portion of pronotum, lateral and central portions of mesonotum, trochanter and proximal portions of mesothoracic legs, lateral and enlarged central portions of mesonotum, proximal part of metathoracic legs, dorsum of abdomen and entire sternum, all brownish-yellow Eyes, head capsule (with exception of Y-shaped suture), anterior plates of pronotum, lateral plates of mesonotum, coxae of mesothoracic legs, small lateral plates of metanotum, coxae of metathoracic legs, pro-, meso- and metathoracic legs dull cupreo-brown

Structural peculiarities — Antennae, four-segmented, second segment bearing two bristles and much smaller than first, third, or fourth Pronotum with two bristles just caudad to eyes Front tarsi two-segmented, hairy Trochanter of mesothoracic legs bearing two prominent bristles, tarsi one-segmented Femur of metathoracic leg twisted, tarsi one-segmented Abdomen with seven segments, dorsal portion of eighth present

SECOND INSTAR

Size — Length of body 1 023 1 113 mm Width of head, including eyes, 0 534–0 581 mm (preserved material) (See Fig 6)

Shape — Slightly rounded, width of mesothorax slightly greater than one half of length of body Length of prothorax slightly greater than one third of length of abdomen Width of head, including eyes, one fourth greater than abdomen at widest part General form of body slightly oblong, subquadrate, interrupted by distinct indentation between meso- and metathorax

Color -- Basal segment of antennae, Y-shaped head suture, median and extremely lateral portions of pronotum, trochanter and femora of prothoracic legs, narrowly median and widely lateral parts of mesonotum, trochanter and proximal parts of mesothoracic legs, median portion widening posteriorly and lateral margins of metanotum, trochanter and proximal portion of metathoracic legs, wide median and narrow lateral parts of abdomen, and ventral side of thorax all a dull cupreous yellow Head capsule, inner lateral plates of pronotum, coxae and tarsi of prothoracic legs, wide lateral plates of mesonotum, coxae, distal parts of femora, tibiae and tarsi of mesothoracic legs, lateral posteriorly narrowed metanotal plates, coxae, distal portions of femora, tibiae and tarsi of metathoracic legs, posteriorly narrowed abdominal plates, and extreme tip of abdomen, a dull bronzed brown Last three segments of antennae varying in intensity of brown from the second to the last Eyes reddish-brown

Structural peculiarities — Antennae, four-segmented, first and third segments of almost equal length, second segment one half of length of fourth, third segment supporting two very prominent hairs Tylus with one small hair on either side at base One prominent hair on either side of head at origin of Y-shaped suture Two bristles on prothorax just posterior to each eye Front tarsi two-segmented, first tarsal segment hidden, second with two bristles on the subapical end Tibia bearing two bristles on under side Beak three-segmented, apical end inserted between coxae of prothoracic legs Three prominent hairs on the middle trochanter, tarsi one-segmented, ventral side of middle trochanter with small cavity surrounded by hairs Hind femora twisted in proximal upper third, tarsi one-segmented, abdomen with seven segments

THIRD INSTAR

Size — Length of body 1 302 1 698 mm Width of head including eyes 0 581 0 639 (preserved material) (See Fig 5)

Shape – Female, oblong, tapering at the posterior end Male slightly rounded, subtruncate at posterior end Indentation between meso- and metathorax more pronounced in male than female Male, length of body slightly more than half the width of mesothorax Female, length of body less than two thirds greater than width of mesothorax length of prothorax one fifth of length of abdomen Male, length of prothorax greater than one third of length of abdomen, width of head, including eyes, only slightly greater than width of abdomen Female, width of head, including eyes, equal to width of abdomen

Color — Proximal portions of first and third antennal segments, Y-shaped suture on head, of male and female a dull brownish-yellow Wide median and narrow margins of pronotum, trochanter and femora of prothoracic legs, median portion widening posteriorly, and lateral parts of mesonotum, trochanter and proximal portions of femora of mesothoracic legs, middle portion widening posteriorly and connecting with lateral portions one half of length of metanotum connecting very narrowly with lateral parts, trochanter and proximal parts of metathoracic legs, median and lateral portions of abdomen (median widening posteriorly and extending to lateral part on each segment, with slight increase in each posteriorly), and last segment of abdomen in female all a dull brownish-yellow Distal portion of first and third antennal segments, second and fourth antennal segments, head capsule, distinct plates of pronotum, coxae and tarsi of prothoracic legs, lateral plates of mesonotum and narrowing posteriorly, mesothoracic coxae, distal portions of mesothoracic legs, lateral plates of metanotum narrowed posteriorly and interrupted near center *for slight space, metathoracic coxae, distal four fifths of femora,* all tibiae, tarsi of metathoracic legs, dorsal lateral plates decreasing from the first to the seventh, and apical end of female abdomen, all a cupreous brown Lateral and median portions of mesonotum, lateral parts of metanotum, lateral portions of abdomen, trochanter and proximal parts of pro-, meso- and metathoracic legs, a dull brownish-yellow Remaining parts of body with exception of eyes, dull cupreous brown Eyes in male and female reddish-brown

Structural peculiarities — Antennae, four-segmented, first and fourth segments thickened in the male, first and third of almost equal length, first slightly longer in male, second segment one third of length of fourth in male, second segment slightly less than one half of length of fourth in female, third segment of antennae bearing three prominent bristles Base of tylus with one hair on either side Two hairs on either side of head at origin of Y-shaped suture Two pairs of hairs just anterior to eyes, two pairs of hairs just posterior to eyes Front tarsi two-segmented Tibiae bearing three bristles on ventral side First segment of tarsus almost hidden, second elongate, notched on inner side, notch bearing two prominent hairs Beak three-segmented, apical end inserted between prothoracic legs Middle trochanter bearing few obvious hairs, excavated on ventral side, mesothoracic tarsi one-segmented Hind femora twisted in proximal portion, enlarged greatly in male, on apical end, usual form in female Metathoracic tarsi one-segmented Abdomen seven-segmented, in male rounded and enlarged posteriorly, in female tapering equally to point First instar to show sexual dimorphism

FOURTH INSTAR

Size — Length of body 1 581–1 907 mm Width of head, including the eyes, 0 767–0 790 mm (See Fig 4)

Color — Variable, resembling closely that of the third instar nymphs (preserved material)

Structural peculiarities — Sexual dimorphism exhibited as in third instar Morphological characteristics not changing in form, dimensions increasing in proportion to size of insect Differences in third and fourth instar fourth has more bristles, mesonotal plates reduced, metanotal plates increased, abdominal plates much more obvious, abdomen of male rounded posteriorly

FIFTH INSTAR

Size — Length of body 2 326-2 465 mm Width of head, including the eyes, 0 884 0 907 mm (preserved material) (See Fig 3)

Color — Variable, resembling very closely that of the fourth and third instars (preserved material)

Structural peculiarities — Sexual dimorphism exhibited as in two previous instars Characteristics not altering except in proportion to growth in size A few essential points of differentiation are greater abundance of bristles, reduction of pronotal plates, enlargement of mesonotal plates, reduction of metanotal plates, abdominal plates more apparent, middle tarsi two-segmented, hind tarsi two-segmented, posterior end of abdomen of male more elongate, posterior end of abdomen of female with more unequal tapering, the apical end being elongate and tapering more distinctly than other parts

ADULTS

Size — Female, length of body 3 488 mm Width of head, including the eyes, 0 943 0 963 mm Male, length of body 2 920 2 948 mm Width of head, including the eyes, 1 011-1 019 mm (preserved material)

Good descriptions of both male and female are published in many well-known works on the Hemiptera, so that the writer will not repeat them There has been one report of collecting a winged form of *R rileyi*, but none was found on Bessey Creek The cover of the *Proceedings of the Entomological Society of Washington* has a picture of this form

UNIVERSITY OF MICHIGAN

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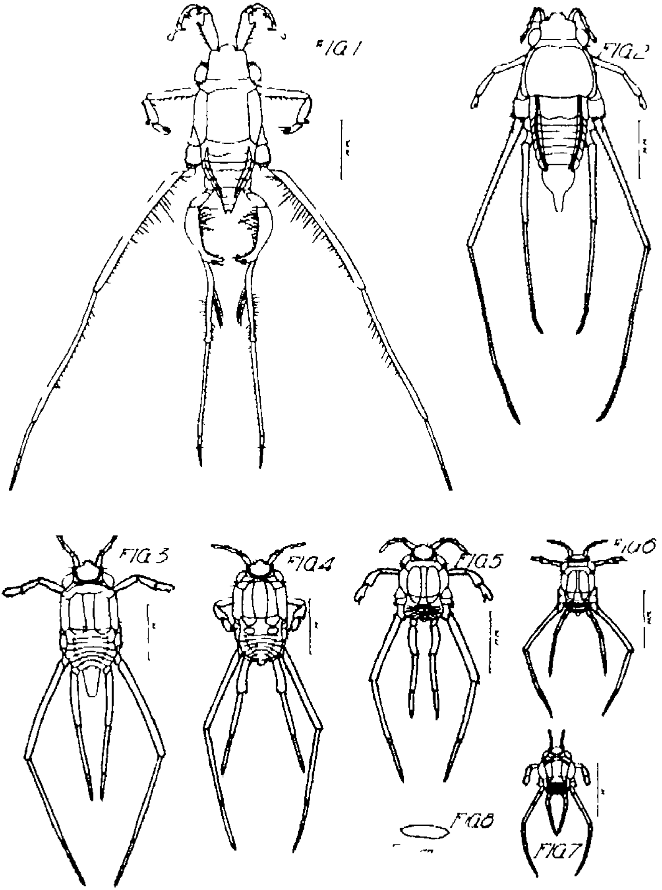
PLATE XL



Rheumatobates rileyi (Berg.)

Fig. 1 Male
Fig. 2 Female
Fig. 3 First instar
Fig. 4 Second instar
Fig. 5 Third instar
Fig. 6 Fourth instar
Fig. 7 Fifth instar
Fig. 8 Egg

STUDIES ON THE TREMATODE FAMILY STRIGEIDAE (HOLOSTOMIDAE) NO XXII *COTYLURUS FLABELLIFORMIS* (FAUST) AND ITS LIFE-HISTORY *

JOHN P VAN HAITSMA

PART I THE ADULT

THE trematode species of the family Strigeidae here described as *Cotylurus flabelliformis* (Faust) was first found in wild and domestic ducks of Michigan during the summer of 1925 Adult parasites of this species have a distinct cup-shaped forebody (Figs 11 and 12), inside of which there are lateral sucking cups, characters which place these parasites in the subfamily Strigeinae Railliet, 1919 This species is further characterized by a tongue-shaped process projecting from the antero-ventral wall of the bursa copulatrix and by the distribution of its vitellaria, which are confined to the hindbody These two characters determine the place of this species in the genus Cotylurus Szidat, 1929

No species of Cotylurus has thus far been described from ducks of North America, although Rettger (1897, pp 224–225) has reported the finding of holostomes in ducks of Indiana The material which I secured from American ducks has been carefully compared with two descriptions of similar parasites of Europe that of *Strigea tarda* by Mathias (1925, pp 1–65) and of *Cotylurus cornutus* by Szidat (1929, pp 736–739) According to Szidat, *S tarda* is an objective synonym of *C cornutus* Sufficient differences in size and structure were found to justify the description of my material as a new species By means of infection experiments, to be described in Part II of this paper, I have proved that the adults of this species develop from *Tetracotyle flabelliformis* Faust, 1917 (March), which in turn developed from *Cercaria douglasi* Cort, 1917 (December) According to the rules of nomenclature, the name of this species, therefore, becomes *Cotylurus flabelliformis* (Faust), a name taken from the first described stage of its life-cycle

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* Contribution from the Biological Laboratory of Calvin College and from the Biological Station and the Zoölogical Laboratory of the University of Michigan This is the twenty-second of a series of studies on the family Strigeidae by Professor George R. La Rue, his students and associates

OCCURRENCE AND DISTRIBUTION OF NATURAL INFESTATIONS

In 1925 *C flabelliformis* was found in domestic ducks on poultry farms both north and south of Grand Rapids, Michigan, and in domestic ducks raised at Ingleside, Michigan The ducks south of Grand Rapids in which this parasite was found lived in a swampy area that contained only temporary pools A search of the ground of this area revealed the shells of several species of small snails Some of them probably served as intermediate hosts of the parasite, but they could become infested with this species only when the swampy ground contained enough water to maintain the aquatic stages of the parasite This fact suggests the possibility that the eggs of this species may remain viable in moist soil for some time

A careful comparison of materials showed that probably the same species of Cotylurus was present in two wild ducks also, a black duck, *Anas obscura* Gmelin, at Grand Rapids, Michigan, and a lesser scaup duck, *Marila affinis* (Eyton), at Holland, Michigan During the autumn migrations of 1926 and 1927 a similar parasite was found at Warsaw, Illinois, in a red-legged black duck, *Anas rubripes* Brewst , a pintail duck, *Dafila acuta* (Linn), a lesser scaup duck, *Marila affinis* (Eyton), five specimens of golden eye, *Clangula clangula americana* (Bonaparte) and two shoveler ducks, *Spatula clypeata* (Linn) The ducks from Illinois were identified by Mr Earl Lambert, who kindly sent me their intestines in a fixed and preserved condition Owing to the fact that the specimens of Cotylurus of all the wild ducks had been dead for some time before they were fixed and preserved, I cannot be entirely certain that they are of the same species as the ones obtained from the domestic ducks, although they appear to belong to it If this interpretation is correct, the finding of this species in ducks from these localities indicates that it is widespread in this country From the foregoing records of its distribution it seems probable that *C flabelliformis* may be found in ducks of any region of North America containing swampy areas, lakes, ponds or streams which are visited by wild ducks during their migrations

SPECIFIC DIAGNOSIS

Cotylurus flabelliformis (Faust) — Characters of the genus, forebody distinctly set off from the hindbody by a deep groove, forebody nearly spherical, 0 20–0 28 mm long, *strongly flexed upon the slightly curved, cylindrical hindbody,* the latter, 0 36–0 57 mm long, broadly truncate at the posterior end, diameter of the forebody, 0 22–0 32 mm , of the hindbody, 0 20–0 26 mm , one to four lappets of the holdfast organ often protruded from the opening of the forebody, oral sucker terminal, 0 05–0 07 by 0 04–0 08 mm , nearly equal to the acetabulum, 0 06 0 08 by 0 04 0 08 mm , ovary, flattened-ellipsoidal, mean diameters 0 109 by 0 066 by 0 051 mm , situated in the anterior fourth of the hindbody, the testes, in anterior view bean-shaped deeply incurved at the hilus, in lateral view heart-shaped with the apex directed dorsally, vasa efferentia united into vas deferens in front of anterior testis, eggs, after laying, 0 10 -0 112 by 0 068 0 076 mm , habitat, intestines of domestic and wild ducks of North America

DESCRIPTION OF THE ADULT

The adult *C flabelliformis* differs in several respects from the adult *S tarda* as described by Mathias The description of *S tarda* by Mathias is general, however, and lacks many details of taxonomic value, so that a nice comparison is impossible On this account also no attempt is made here to locate *S tarda* in the revised classification of Szidat and the name *S tarda* is retained for Mathias' species Szidat makes *S tarda* synonymous with *C cornutus*, but the discussion presented in this paper will show that such synonymy does not follow from Mathias' description

The more significant differences between *C cornutus* and *C flabelliformis* will also be indicated

External features — The body of *C flabelliformis* is divided by a deep constriction into two body regions, a cylindrical hindbody and a cup-shaped forebody, the former twice as long as the latter The body is usually strongly flexed at the junction of the body regions, so that the forebody appears to be attached to the antero-dorsal side of the hindbody Neither Mathias nor Szidat describes such a marked body flexure for their species and their figures do not indicate it Often the dorsal side of the forebody is extended and its ventral side is contracted so that the opening of the cup appears to be on its ventral surface (Fig 11) Both these conditions are only apparent, however, since the forebody is attached to the anterior end of the hindbody and the opening of the forebody is in reality at its anterior end From the opening of the forebody in many specimens one to four lappets of the holdfast organ may protrude The general color of the body is white, except that along the ventral half of the hindbody there is a brassy-colored area, indicating the location of the brownish vitellaria within The opening of the bursa copulatrix or genital pore is large and funnel-shaped, and located on the dorsal surface near the posterior end of the hindbody In some specimens grooves are found near the posterior end of the hindbody Their presence and extent doubtless depend upon the degree of dilatation of the excretory spaces near them

Measurements — Comparative measurements of *C flabelliformis* and of *S tarda* (measurements by Mathias, 1925, pp 25-26) are presented in Table I The measurements of *C flabelliformis* were recorded from egg-laying specimens obtained from a duck which was infested daily from July 18 to August 5, 1926 On the latter date the duck was killed and the intestine with its contents was fixed in corrosive-acetic in the usual manner The specimens appeared to be normal, with no evidence of extraordinary shrinkage Specimens larger than the ones measured were not collected from any of my feeding experiments Although the details of Mathias' technique are not given and although he does not explain how his measurements were made, it seems improbable that

TABLE I MEASUREMENTS OF *C flabelliformis* IN MM AS COMPARED WITH THOSE OF *S tarda* AFTER MATHIAS

Item	Number measured	*C flabelliformis*				*S tarda*	
		Range	Mean	Smallest specimen	Largest specimen	Type specimen	After Mathias*
Total length †	10	0 56–0 85	0 716	0 56	0 85	0 68	0 90–1 98
Forebody							
Length ‡	10	0 20–0 28	0 239	0 20	0 28	0 24	0 40–0 60
Dorso-ventral diameter	10	0 22–0 32	0 278	0 26	0 32	0 28	0 56–0 72
Hindbody							
Length	10	0 36–0 57	0 477	0 36	0 57	0 44	
Dorso-ventral diameter §	10	0 20–0 26	0 258	0 20	0 26	0 23	
Oral sucker							
Length	10	0 05–0 07	0 059	0 055	0 06	0 06	0 09–0 109
Dorso-ventral diameter	10	0 04–0 08	0 06	0 05	0 07	0 06	0 09–0 109
Pharynx							
Length	10	0 03–0 045	0 037	0 035	0 038	0 04	
Diameter	10	0 02–0 04	0 03	0 03	0 04	0 025	
Acetabulum							
Length	10	0 06–0 083	0 07	0 06	0 07	0 07	0 112–0 133
Dorso-ventral diameter	10	0 04–0 08	0 062	0 055	0 06	0 07	0 112–0 133
Ovary							
Transverse diameter ‖	10	0 075–0 135	0 109	0 075	0 127	0 09	0 11
Dorso-ventral diameter	10	0 05–0 075	0 066	0 05	0 07	0 07	0 11
Antero-posterior diameter	10	0 04–0 06	0 051	0 04	0 05	0 047	0 058
Uterine egg							
Length	10	0 08–0 10	0 088	0 08	0 08		
Diameter	10	0 04–0 06	0 055	0 05	0 05		
Eggs from feces of duck							
Length	10	0 10–0 112	0 107				0 097–0 117
Diameter	10	0 068–0 076	0 0705				0 062–0 080

* Measurements recorded by Mathias (1925) no statement of method given † Measured upon median sagittal sections ‡ Measured along middle line of median sagittal sections. § Measured immediately behind posterior testis. ‖ An approximation obtained by adding the thicknesses of several serial sagittal sections

differences in methods can account for the wide differences between his measurements and mine Except in the instances noted in the table, the measurements of *C flabelliformis* were made upon carefully selected median sagittal sections of the body regions and organs indicated, because this method seemed to be the most accurate Nearly all the measurements of *C flabelliformis* fall below those of *S tarda*, as determined by Mathias, and of *C cornutus*, as described by Szidat The eggs of these three species resemble one another quite closely in size, but since eggs of several species of Strigeidae are known to have a wide range of size within the species, measurements of eggs can have only small significance in determining species Despite similarities in this character, the wide differences in the other measurements presented in Table I indicate that *C flabelliformis* is distinct from *S tarda* and *C cornutus*

Holdfast organ and adhesive gland — In this species the holdfast organ consists of two transverse lips, an anterior and a posterior, both of which are partly cleft into nearly equal right and left parts or lappets (Figs 10, 12–15) These lappets are contractile and consequently often differ greatly in size in preserved specimens They may extend outside the cup or they may be folded inside in various ways The lips of the holdfast organ may also surround varying amounts of host tissue For these reasons sections of the forebodies of different individuals often present confusingly variable pictures Immediately beneath the holdfast organ there is a rather compact disk-shaped adhesive gland from which large processes of less compact tissue extend into the tips of the holdfast organ In *C flabelliformis* the secretion of the adhesive gland seems to have a corrosive or digestive action, since those parts of the intestinal wall of the host which extend into the cup-like forebody are always denuded of their columnar epithelium Brandes (1890, pp 552, 556), Muehling (1896, p 272), Szidat (1929, p 635) and La Rue (1927, p 226) have expressed similar opinions on the corrosive action of this secretion in other species of Strigeidae The removal of the intestinal epithelium bringing the cuticula of the parasite into direct contact with the vascular tissue of the host doubtless facilitates the absorption of the host's lymph and blood plasma Further support for this theory of nutrition is derived from the fact that no blood corpuscles were found in the digestive ceca of any of the specimens examined

Lateral sucking cups — In metacercariae the lateral sucking cups are thought to be glandular pockets which have no adhesive function, but in the adult of this species these organs become deep pocket-like cavities which are clearly organs of attachment These pockets are situated posterior to and at the sides of the pharynx and they extend posterad to the level of the acetabulum Conspicuous muscle strands extend from the bottoms and sides of the pockets to the dorsal wall of the forebody In sections pieces of host tissue were often seen filling their cavities The host tissue, without its epithelium, was often so closely adjusted to the lateral sucking cup of the parasite that it was difficult to distinguish the boundary between parasite and host The clasping action of the lateral sucking cups, together with the muscular contractions of the forebody as a whole and of the anterior part of the cup-like forebody in particular, serve to attach the parasite to its host

Following the description of Brandes (1890, p 559) for Strigea and of Muehling (1896, pp 270, 272) for Cyathocotyle, I visualize the action of the forebody of the present species in accordance with its structure as follows During the contraction of the circular muscles of the forebody some of the liquid in its excretory spaces is pressed into the hindbody, which therefore becomes turgid Then large muscles extending from the bottom and sides of the cup-like forebody to the organs and dorsal wall of the hindbody contract forcibly and bend the hindbody dorsally against the forebody This action serves to deepen the cup of the forebody and creates a partial vacuum in it and at the same time makes the forebody narrower, so that the wall of the cup and the lips of the holdfast organ are closely pressed against the underlying host tissue This intimate application of the parasite to the tissues of the host permits the absorption of the fluids of the host by the parasite

Digestive system — The digestive system (Fig 10) is like that usually found in the Strigeidae The esophagus is nearly as long as the pharynx In this respect this species differs from *S tarda*, in which the intestinal branches arise immediately behind the pharynx The digestive ceca extend almost to the posterior end of the animal In the hindbody they are situated ventral to the reproductive organs In sections they usually contain a uniformly divided material that stains lightly with eosin and looks like the coagulum of some colloid It is entirely free from the detritus of the intestinal contents of the host, and seems never to contain blood corpuscles or other cellular elements Mathias (1925, p 30) has shown experimentally that *Strigea tarda* ingests liquids and substances in solution, but not solid particles His findings may also explain the uniformity of the material found in the digestive ceca of the present species *C flabelliformis*, therefore, seems to employ two methods of obtaining nourishment first, by the absorption of the nutritive material from the host through the cuticle of the holdfast organ and the inner surface of the cup-like forebody, and second, by the ingestion through the oral sucker and pharynx of some of the liquid contents of the host's intestine or of the digested epithelium of the intestinal wall itself

Nerve strands (Fig 17) — These extend posterad from the pharynx lateral to the digestive ceca of the forebody

Excretory system — As in *Crassiphiala bulboglossa* mihi (Van Haitsma, 1925, p 124), there are four main excretory vessels in the hindbody of *C flabelliformis*, two dorsal and two ventral The two dorsal vessels lie dorsal to the reproductive organs They extend forward from the region of the bursa copulatrix and unite into a single median dorsal vessel near the anterior end of the hindbody Owing to numerous anastomoses with the subcuticular network of excretory spaces on the dorsal side of the animal, they are less distinct than the two ventral vessels, which have fewer anastomoses with the subcuticular excretory network In an early developmental stage of the adult the courses of the dorsal vessels were traced to their junctions with the ventral vessels (Figs 6-8) between the bursa and the posterior testis In sexually mature adults the region between the bursa and the posterior testis is occupied by excretory spaces traversed by numerous parenchyma strands, so that the dorsal vessels here are not so definitely traceable at this stage of development The two ventral vessels of the hindbody are much more definite and distinct than the dorsal vessels, since they anastomose less frequently with the subcuticular excretory spaces These vessels extend, one on the left, the other on the right, along the descending limb of the uterus They correspond to the "Uterusgefasse" which Krause (1914, p 132) described for the hemistomes In the early developmental stage of the adult (Figs 3–6) they connect with a very short common excretory vessel which opens terminally at the excretory pore, but in the sexually mature adult the posterior parts of the two ventral vessels could not be traced to the excretory pore The difficulty here is due to numerous anastomoses with the subcuticular excretory spaces and to the presence of many parenchyma strands which traverse the excretory complex in this region Near the anterior end of the hindbody the two ventral vessels converge and unite to form a short, narrow transverse vessel with which the median dorsal vessel connects (Fig 10)

From this transverse vessel a short median vessel extends anterad along the ventral side of the forebody, where it soon becomes lost in a large complex of excretory spaces A similar but somewhat larger vessel joining the median dorsal vessel of the hindbody extends along the dorsal side of the cup Posterior to the acetabulum this median dorsal vessel of the forebody sends a branch into the anterior lip of the holdfast organ Another small branch extends through the adhesive gland dorso-ventrally and joins the median dorsal vessel of the forebody with the median ventral vessel of the same body region This median dorso ventral vessel of the adhesive gland is also connected with the median dorsal vessel of the hindbody by means of a short antero-posterior vessel that traverses the center of the adhesive gland Two branches from the median dorso-ventral vessel of the adhesive gland extend anterad, one into each lip of the holdfast organ These branches soon divide into secondary branches (Fig 10) whose courses were not completely traced

As in other strigeids, there is also in the present species a peripheral network of excretory spaces in both forebody and hindbody (Figs 3–9, 14–16, 18 20) Along the ventral side of the hindbody they are separated from the ventral vessels by the vitellaria These spaces are larger in the lateral regions of the hindbody than along its ventral side In the posterior part of the dorsal side of the hindbody they may be so large as to make the surface bulge out and thus cause superficial grooves to appear between them (Figs 11-12) For the sake of clearness these peripheral spaces were not represented in Figure 10

Except for the median dorso-ventral vessel of the adhesive gland the pattern of the excretory vessels of *C flabelliformis*, as far as it was traced, agrees in the main with the elaborate results of the study of Thoss (1897, pp 34-42) on the excretory system of *C variegatus* (= *Holostomum cucullus* Thoss) According to Mathias (1925, p 27), the excretory system of *S tarda* consists of a deeply lobed excretory vesicle from each lobe of which a lateral canal extends forward In *C flabelliformis* a definite excretory bladder distinct from the four main canals of the hindbody was not observed Possibly parts of the subcutaneous excretory spaces (Figs 19-20) correspond to the lateral canals of *S tarda* The three-line description of the excretory system of *S tarda* by Mathias, unaccompanied by figures, is too brief to be clear and makes impossible a thorough comparison of the excretory systems of these two species Szidat does not describe the excretory system of *C cornutus*

The functions of the excretory system appear to be more comprehensive than its name implies Since this animal has no distinct circulatory system and since the digestive system seems to be inadequate for the distribution of nourishment to the cells of the body, the distribution of nutriment is probably carried out by the excretory system The assumption of the circulatory function by the excretory system appears still more probable if nourishment is absorbed through the inner wall of the cup-like forebody, as was suggested above

Male genital system — The two testes are located in series and occupy the second and third fourths of the hindbody (Fig 2) In general they are nearly bean-shaped as seen in anterior view, and their concave surfaces are directed ventrally They are also somewhat thinner in their median region than laterally In side view the testes are shaped like hearts with their apices turned dorsally Owing to their irregular shapes, measurements of the testes were not made Their shape differs greatly from that of the testes of *S tarda*, which are described as flattened disks (Mathias, 1925, p 26)

The vasa efferentia arise from the midventral surfaces of their respective testes At first the vasa efferentia are small, inconspicuous ducts, usually free from spermatozoa, but after a short distance they are dilated and made conspicuous by the spermatozoa which they contain These dilatations are not so large and distinct that they deserve the special designation of "seminal reservoirs" The anterior vas efferens (ve_1) arches forward and toward the right over the surface of the anterior testis and then bending backward unites with the posterior vas efferens (ve_2) The posterior vas efferens also bends forward and toward the right from its point of origin and unites with the anterior vas efferens about midway on the ventral surface of the right half of the anterior testis From this point of union of the vasa efferentia the vas deferens extends mesad and posterad between the vasa efferentia On the ventral side of the posterior testis the vas deferens becomes dilated into the large spindle-shaped seminal vesicle This vesicle practically fills the space formed by the arch of the posterior testis Posteriorly and dorsally the seminal vesicle empties into the globular thicker-walled ejaculatory pouch From this pouch the spermatozoa are ejected through a narrow, coiled ejaculatory duct that opens into the genital atrium dorsal to the opening of the uterus The genital atrium opens to the outside through the large genital pore which is located dorsal to the smaller terminal excretory pore The ejaculatory duct traverses a mass of clavate, glandular cells like the cells of Mehlis' gland At first it was thought that these cells represent the prostate gland However, since their function is not definitely known and since they appear to be similar to the subcuticular gland cells (Krause, 1914, p 106), it may not be justifiable to characterize them as a prostate gland Muehling (1896, p 274) describes such a prostate for *Cyathocotyle prussica* Muehling, and Thoss (1897, p 49) a similar one for *C variegatus* (Crepl) The prostate which Brandes (1890, p 563) attributes to the genus Diplostomum appears to be a morphologically different organ and in fact has not been found by recent investigators

According to Mathias (1925, p 26), the vasa efferentia of *S tarda* arise from the anterior parts of their respective testes According to my observations, the vasa efferentia of *C flabelliformis* originate from the midventral points of their testes In fact, the anterior vas efferens could be traced to a point on the anterior testis near the posterior ventral angle of a median sagittal section It is regretted that Mathias does not describe where the anterior and posterior vasa efferentia unite, since the location of this point of junction differs greatly according to the descriptions of different authors, e g Brandes (1890, p 562), Thoss (1897, p 47), Guberlet (1922, pp 10, 12), La Rue (1926, p 29) and Augustine and Uribe (1927, p 239) In *C flabelliformis* the relations of these ducts closely resemble the arrangement as found in *Neodiplostomum cochleare* (Krause), *Diplostomum huronense* (La Rue), *Pharyngostomum cordatum* (Diesing) according to La Rue, and *Alaria arisaemoides* Augustine and Uribe (references above) The close similarity in the arrangement and connections of these ducts in five genera of the Strigeidae makes the descriptions of Brandes for Strigeidae, of Thoss for *C variegatus*, and of Guberlet for *D gavium* and *D confusum* appear doubtful Mathias does not describe the presence of an ejaculatory pouch and an ejaculatory duct in *S tarda* In *C flabelliformis* these ejaculatory organs are readily distinguished from the seminal vesicle, since they are thicker-walled

Szidat (1929, p 646) describes the course of the male genital ducts as follows "Nur bei der Gattung *Cotylurus*, soweit ich feststellen konnte, verlaufen die Ausführungsgänge des männlichen Geschlechtsapparates einfacher Hier zieht das Vas efferens des oberen Hodens sogleich nach unten und nur dasjenige des unteren Hodens hat noch die Richtung nach oben beibehalten (Abb 13) Die beiden Vasa efferentia vereinigen sich hier etwa in Höhe des Dotterreservoirs " Szidat's Figure 13 of *C cornutus* entirely confirms his description It has already been explained why this course of the male genital ducts seems improbable, but if one assumes that Szidat's description of these ducts is correct, it clearly indicates that *C flabelliformis* is a distinct species The different course of the male genital ducts of *C flabelliformis* also demonstrates that Szidat s conception of the course of these ducts in *C cornutus* is not universally characteristic of the genus Cotylurus Szidat recognized a muscular ejaculatory duct in *C cornutus*, but did not distinguish an ejaculatory pouch

Female genital system (Fig 1) – The ovary is ovoid and lies on the anterior testis in the median region of the body The oviduct, arising from the posterior side of the ovary, usually forms a vertical coil before it gives rise to Laurer's canal However, when the hindbody straightens this coil disappears Laurer's canal extends along the middorsal line to the region between the two testes where it opens to the outside The oviduct accompanies Laurer's canal along its ventral side, but in the region between the two testes it turns sharply ventrad into Mehlis gland Here the oviduct is joined by the common vitelline duct and then becomes the ootype which extends through Mehlis' gland from right to left From Mehlis' gland the ascending limb of the uterus continues ventrad and anterad between the posterior vas efferens and the vas deferens along the right side of the ovary to the anterior end of the hindbody Bending abruptly ventrad and posterad it continues, as the descending limb of the uterus, in the median plane to the posterior end of the hindbody It extends throughout its length between the two ventral excretory vessels and in the region of the posterior testis lies ventral to the vas deferens It opens into the genital atrium immediately ventral to the opening of the ejaculatory duct

Mehlis' gland lies between the testes In *C flabelliformis* it is less compact than in some other species of Strigeidae and consequently the fibrous network which binds its single-celled glands together is more readily observed in this species In *C flabelliformis* it consists of a large irregular mass of glandular cells Mathias did not see Mehlis gland in *S tarda*

The vitellaria are found in a single field along the ventral half of the hindbody between the intestinal ceca and the subcuticular excretory spaces The rather large follicles are connected with the vitelline reservoir by means of right and left vitelline ducts, which cross the inner sides of the digestive ceca Unless they contain vitelline material these small ducts are easily overlooked The vitelline reservoir located on the left of Mehlis' gland is nearly triangular both in anterior and sinistral views Near its dorsal angle the vitelline reservoir gives rise to the common vitelline duct, which extends dorsad and dextrad around the oviduct and then bending ventrad and sinistrad empties into the oviduct

Genital atrium — This is the cavity of the bursa copulatrix It is irregular in shape, principally owing to a broad, tongue-shaped muscular process extending inward from its anterior wall ventral to the opening of the uterus This muscular process is Szidat's chief distinguishing characteristic of the genus Cotylurus This process ordinarily nearly fills the genital atrium in *C flabelliformis* Its function is not definitely known, but it appears to be of a special nature, since it is not present in all species of Strigeidae (Krause, 1914, p 190, and Van Haitsma, 1925, p 126) Its structure and position suggest that it may function during the extrusion of the egg or during copulation Mathias does not mention it in his description of *S tarda* According to the only record of observed copulation in the Strigeidae (Brandes, 1890, p 566), the bursa copulatrix serves as a copulatory organ

SYNOPSIS OF DIFFERENCES BETWEEN *C* AND MATHIAS' DESCRIPTION OF *S tarda*

1 Measurements of *C flabelliformis*, the whole organism, the body regions and various organs, fall below the limits of corresponding measurements of *S tarda*

2 In *C flabelliformis* the esophagus is nearly as long as the pharynx (Fig 17) In *S tarda* the intestinal branches arise immediately behind the pharynx

3 There are four main excretory vessels in the hindbody of *C flabelliformis*, two dorsal and two ventral Near the posterior end of the hindbody these vessels anastomose without forming a distinct excretory bladder The excretory system of *S tarda* consists of a deeply lobed excretory bladder, from each lobe of which a lateral excretory canal runs forward

4 The testes of *C flabelliformis* are bean-shaped organs, thinner medially than laterally The testes of *S tarda* are flattened disks

5 A Mehlis gland appears to be lacking in *S tarda* In *C flabelliformis* an irregularly shaped Mehlis gland is found in the usual position

6 A muscular tongue-shaped process extends into the genital atrium of *C flabelliformis* Mathias does not mention such a process for *S tarda*

PART II LIFE-HISTORY

DURING the present decade several life-history studies in the family Strigeidae have been made in South America (Lutz, 1920) and Europe (Ruszkowski, 1921, Mathias, 1922, Szidat, 1923 and 1924), but such a study has thus far not been made in North America While the present study of the life-history of *Cotylurus flabelliformis* (Faust) was in progress, the dissertation of Mathias (1925, pp 1-65) on the "Cycle évolutif d'un trematode holostomide, *Strigea tarda* (Steenstrup)" became available This work of Mathias offered the opportunity to make comparisons in the life-histories of two structurally similar species of different continents, *S tarda* of Europe and *C flabelliformis* of North America A comparative morphological description of these two species has already been made in Part I of this paper

Snail hosts — Since *C flabelliformis* resembles *S tarda* in form and structure and was found in similar definitive hosts, it was presumed that the life-histories of these two species would not differ greatly Therefore various snails of Douglas Lake were examined for tetracotyles resembling those described as *Tetracotyle typica* Diesing, the metacercaria of *S tarda* (Lühe, 1909, p 163, Szidat, 1923, p 310) Such tetracotyles were found in *Lymnea humilis* Say, *L reflexa* Say, *L stagnalis appressa* Say, *L stagnalis perampla* Walker, *L emarginata angulata* Sowerby and *Planorbis trivolvis* Say Hughes (1929, pp 495-508) described these tetracotyles from the same species of snails of the same lake as *Tetracotyle flabelliformis* Faust

TABLE II

FEEDING EXPERIMENTS

Record number of experiment	Record number of duck	Tetracotyles or snails fed	Period of feeding	Death of host	Results
Group A					
I	111	About 100 *P trivolvis*	July 20–July 25 1925	Died July 25 1925	100+ Cotylurus mature and immature
II	113	About 100 *L emarginata angulata*	July 18–July 25 1925	Died July 25 1925	100+ Cotylurus, mature and immature
III	130	About 200 *L stagnalis appressa*	July 18–Aug 5 1925	Killed Aug 5 1925	100+ Cotylurus mature and immature
IV	171	**L emarginata angulata*	July 10 1926	Killed July 16 1926	No Cotylurus no fecal examination
	202	**L emarginata angulata*	July 10, 1926	Killed Aug 10 1926	No Cotylurus, no fecal examination
	217	**L emarginata angulata*	July 10 1926	Killed Oct 7 1926	No Cotylurus, no fecal examination
V	186	† *L stagnalis appressa* and *P trivolvis*	July 1–Aug 2 1926	Killed Aug 2 1926	100+ Cotylurus, mature and immature
	212	† *L stagnalis appressa* and *P trivolvis*	July 1–Aug 7 1926	Killed Aug 28, 1926	No Cotylurus, but collected eggs
	214	† *L stagnalis appressa* and *P trivolvis*	July 1–Aug 7, 1926	Died Sept 7 1926	No Cotylurus, but collected eggs
VI	248	60 *L stagnalis appressa*	July 28–Aug 3 1927	Killed Aug 4 1927	25+ Cotylurus, mature and immature

TABLE II (*continued*)

Group B					
VII	232	20 tetracotyles without cyst-like coverings from *L stagnalis appressa*	July 11 1927	Died July 14 1927	No Cotylurus no fecal examination
VIII	254	30 tetracotyles without cyst-like coverings from *L stagnalis appressa*	Aug 4 1927	Killed Aug 8 1927	No Cotylurus, no fecal examination
IX	246	235 tetracotyles with cyst-like coverings from *L reflexa*	July 2–July 23 1927	Died Aug 3 1927	No Cotylurus but eggs were collected on July 9
X	269	40 tetracotyles with cyst like coverings from *L stagnalis appressa*	Aug 9 1927	Killed Aug 15 1927	No Cotylurus, no fecal examination
Group C					
XI	270	13 *L stagnalis appressa* all tetracotyles have cyst-like covering	Sept 6 7 1927	Killed Sept 10 1927	200+ Cotylurus, mature and immature also eggs collected on Sept 10

* Five snails to three ducks
† Five hundred and twenty-nine snails to three ducks

General technique of experiments — During the summers of 1925, 1926 and 1927 the four species of snails last mentioned were selected for eleven feeding experiments involving fifteen domestic ducks, as recorded in Table II During the course of the experiments the ducks, from three to seven weeks old, were carefully guarded against other than purposive strigeid infestations They were kept on sand in pens screened with poultry netting, about four hundred feet from the lake shore, where it was impossible for them to obtain any materials which might contain strigeid metacercariae except those fed No attempt was made to screen the ducks against insects, since there are no records of the finding of metacercariae of the Strigeidae in insects The food of the ducks consisted of bread, lettuce, table scraps, prepared chick mash, and bread and milk mixed with sand Occasionally a few scraps of fresh beef were also fed The drinking water was pumped from a well The snails fed to the ducks in the experiments were always crushed just before feeding When tetracotyles alone were to be given to the ducks they were picked from the crushed snails, examined and sorted microscopically and introduced into the ducks either by means of a pipette or by placing them in small cavities formed in pieces of beef, which the birds ate greedily The feces of the ducks were examined for strigeid eggs at the beginning of each experiment to determine whether the birds were free from parasites Fecal examinations were also made at intervals during some of the experiments either for the purpose of collecting the eggs or to watch the progress of an infestation At the end of each experiment and at different intervals after the last experimental feeding the ducks were killed and their intestines were examined for their trematode populations Thereupon the intestines with their contents were shaken in water for three minutes, then in corrosive-acetic for one-half minute, and five or more hours later any trematodes that were present were sorted out of the intestinal contents, washed in water, and preserved in 70 per cent alcohol with glycerine

Grouping and general description of experiments — According to the materials fed my infestation experiments fall into three groups, A, B and C In group A, experiments I–VI, naturally infested snails from Douglas Lake were fed to ten ducks The experiments of group B consist of two subgroups, B′ and B″ In subgroup B′, experiments VII and VIII, tetracotyles without cyst-like coverings were removed from the snails and fed to two ducks, in subgroup B″, experiments IX and X, encysted tetracotyles were similarly removed from snails and fed to two ducks In group C, experiment XI, snails experimentally infested with *Cercaria douglasi* Cort, 1917, were fed to one duck The experiments of group A were made during the summers of 1925, 1926 and 1927 They prove that tetracotyles naturally infesting snails of Douglas Lake develop into adult *C flabelliformis* in the domestic duck The experiments of group B showed that encysted tetracotyles of this species continued their development in the domestic duck while the tetracotyles without cyst-like coverings did not develop The experiment of group C demonstrated not only that *Tetracotyle flabelliformis* Faust, 1917 (March), continued its development in the domestic duck, but also that this tetracotyle itself developed in the snails from *Cercaria douglasi* Cort, 1917 (December) In order to evaluate the significance of these groups of experiments it will be necessary to discuss them in somewhat greater detail

Group A

Experiments I, II and III The ducks of these three experiments were infested with trematodes when they came into my possession This was determined by fecal examinations before the feedings began In the feces of each of the three ducks a small number of strigeid eggs were found The history of these ducks during the three days previous to the fecal examinations was known to have been such that infestation during that time was impossible During two of the three days the ducks were in transit and on the third day they were in the pens and cared for as related in the general description of technique My later investigations have shown that *C flabelliformis* attains the egg-laying stage in about three days after entering the duck Hence, if the trematodes present in these ducks were *C flabelliformis*, they all must have attained the egg-laying stage before the beginning of the experiments Since the fecal examinations revealed only a few eggs, it is probable that the number of strigeids present in the ducks at this time was small During these three experiments, I, II and III, snails containing tetracotyles were fed daily to the ducks until the time of their death On the fourth day after the first feeding with the snails the number of eggs in the feces of the ducks had increased very greatly There is no doubt that this increase was due to a greater number of adult worms secured from the snails fed Moreover, in each of these experiments specimens of *C flabelliformis* were finally obtained in all stages of development from slightly modified tetracotyles to the egg-laying adults The finding of this graduated series of stages in all three experiments is conclusive proof that increased infestation resulted from the experimental feeding

Experiment IV — This experiment of group A was not successful Five snails containing tetracotyles were fed to three ducks on one day Circumstances prevented the carrying out of this experiment as originally planned No fecal examinations were made and the ducks were killed and examined more than a month after the experimental feeding At this time these ducks were parasite-free

Experiment V — Since the three ducks of this experiment were under my care from day-old ducklings until their death, this is a critical experiment One of the ducks was fed snails containing tetracotyles from the time that it was three weeks old until it was killed five weeks later Examination of its intestines revealed that it contained more than one hundred specimens of mature and immature *C flabelliformis* The record of this duck, therefore, shows without question that the tetracotyles in the snails developed into adults in the domestic duck Fecal examinations during the course of the feeding of the other two ducks showed that they also became infested Owing to the belief that the adults obtained from experiments I, II and III of group A were not full-grown, the two remaining ducks of this experiment were kept about one month after the last feeding of snails to permit their parasites to grow to a larger size, but at the time of their death they had become parasite-free

Experiment VI — The duck of the last experiment of group A was six to seven weeks old at the time when the experimental feeding began During the last two weeks previous to this time it had been under my care The conditions under which it lived before it came under my care are not known Absence of eggs from the feces at the beginning of the experiment showed that it was parasite-free By actual count sixty *Lymnea stagnalis appressa* were fed to it during the six days prior to its killing The post-mortem examination revealed twenty-five mature and immature *C flabelliformis* in its intestines The result of this experiment agrees, therefore, with the results of experiments I, II, III and V

Conclusions from the experiments of group A — The preceding experiments, constituting group A, show that tetracotyles in *L stagnalis appressa*, *L stagnalis perampla*, *L emarginata angulata* and *Planorbis trivolvis* are able to develop to maturity in the domestic duck These tetracotyles, although found in four kinds of snails, belong to one species because they develop into one kind of adult Since they were found in the snails early in the summer as soon as the snails came up from deep water, it seems probable that this species passes the winter in the snail in the tetracotyle stage The number of adult parasites recovered from the ducks for each snail fed is small The duck of experiment VI was older than the ducks of the other experiments and the ratio of adults recovered from it as compared with the number of tetracotyles fed was smaller than in the experiments with the younger ducks This result agrees with the belief already held that older ducks are less readily infested than younger ones

Group B

General considerations — In the snails of the experiments of group A two kinds of tetracotyles were found, some with thick, gelatinous, cyst-like coverings and others without such coverings, but only one kind of adult was obtained from the ducks to which both kinds of tetracotyles were fed Therefore the experiments of group B (VII, VIII, IX and X) were devised to determine which of these kinds of tetracotyles, those with or those without the thick coverings, had developed in the ducks of group A They were removed from the snails and sorted as already described The collection of a dose of tetracotyles required from one to two hours, during which time they were kept in water in watch glasses The doses were given to the ducks imbedded in small pieces of beef, or in water by means of a pipette The ducks of these experiments were under my care more than a week before the experimental feedings began Fecal examinations during this time showed that all of them were free from parasites

Experiments VII and VIII — Small doses of tetracotyles without cyst-like coverings were given to the ducks of experiments VII and VIII and a few days later the ducks were examined *post mortem* for the Cotylurus they might contain No parasites were found in either duck The most probable explanation of this result is that tetracotyles without the cyst-like coverings were too immature to continue their growth in the domestic duck Conclusive evidence will be presented in connection with the discussion of experiment XI of group C to show that tetracotyles without cyst-like coverings develop into tetracotyles with cyst-like coverings *A priori* it seems probable that the thick gelatinous covering is essential for the protection of the delicate tetracotyle against the grinding and digestive power of the gizzard of the duck The interpretation that tetracotyles without cyst-like coverings are too immature to develop in the duck is supported by von Linstow (1894, p 332), who described the formation of a similar cyst for *Tetracotyle typica* and expressed the belief that *Tetracotyle typica* can become sexually mature in vertebrates only after the cyst is formed There is, therefore, sufficient reason to believe that tetracotyles without cyst-like coverings cannot develop in the domestic duck, yet it must also be admitted that experiments VII and VIII, owing to the small number of tetracotyles fed, were not sufficiently critical to establish this belief beyond all doubt

Experiments IX and X — In each of these two experiments tetracotyles with cyst-like coverings were fed to a duck To duck 246 of experiment IX two hundred and thirty-five were fed during a period of three weeks, July 2 to July 23 On July 9, just one week after the feeding began, strigeid eggs were observed in its feces, proving that tetracotyles with cyst-like coverings had developed into adults, yet at the autopsy of the duck on August 3, eleven days after the last experimental feeding, no parasites were found in its intestine Presumably the period of eleven days was longer than the life of the parasites in the duck In experiment X only forty tetracotyles with cyst-like coverings were fed to a duck on one day, August 9, and six days later, on August 15, the duck was killed At the post-mortem examination no parasites were found Their absence needs to be explained

The explanation for the negative result of experiment X is suggested by my previous experiments, namely, that too few tetracotyles were used in feeding All my feeding experiments show that only a small percentage of the tetracotyles ingested by the ducks underwent development In the experiments giving positive results the number of tetracotyles fed was always many times greater than the number of adults obtained and in experiments involving small numbers of tetracotyles infestation did not take place at all Although the number of tetracotyles in each of the snails fed is not known, an actual count of the number found in thirteen snails by Hughes (1929, p 495) gave an average of one hundred and eighteen per snail Hence an average of fifty fully developed tetracotyles in each snail is a conservative estimate On the basis of this estimate less than two per cent of the tetracotyles fed develop to maturity in the domestic duck For this reason experiments IV, VII, VIII and X do not give conclusive results At most, there is only a slight indication in experiments VII and VIII that tetracotyles without cyst-like coverings do not develop in the domestic duck That tetracotyles with cyst-like coverings do develop in ducks is clearly demonstrated by my experiment IX and also, as will be shown later, by experiment XI

Group C

Life-history experiment Experiment XI — The development of *Cercaria douglasi* Cort into adult *C flabelliformis* has been demonstrated thus During the summer of 1927 Professor W W Cort permitted me to utilize the results of his experiments on the development of *Cercaria douglasi* in snails A brief note concerning these experiments has been published (Cort and Brooks, 1928, p 194) The details are as follows A lot of snails, *L stagnalis appressa* Say and *L stagnalis perampla* Walker, were collected from a limited area of the north shore of Douglas Lake Twenty-five, used as controls, were examined for tetracotyles, but none of them showed an infestation From July 26 until July 29 forty were exposed to large numbers of cercariae At intervals Professor Cort killed and examined a few and in this way was able to watch the development of the penetrated cercariae into the mobile metacercaria stage, i e the stage before the thick gelatinous covering was formed On August 17 examination of three snails indicated that all the cercariae had attained this stage of development All of Professor Cort's observations showed that the metacercariae resulted only from his experimental infestations

On August 19, 1927, Professor Cort generously turned over to me twenty-eight of these snails which had been experimentally infested about three weeks before They were carefully tended until September 6, but in spite of excellent care fourteen died during this time On the 6th and 7th of September, about six weeks after their exposure to *Cercaria douglasi*, thirteen of the fourteen remaining snails were examined After removal of the shell the posterior twisted part of the body of each snail was teased apart and the tetracotyles present were studied under the dissecting microscope The number in each snail was extraordinarily large, much larger than the number usually found in naturally infested snails of Douglas Lake Apparently the tetracotyles were identical with those employed in my former experiments Every one observed possessed a thick gelatinous covering After the examination of each snail it was immediately fed, together with its tetracotyles, to a five-week-old duck (number 270 of experiment XI in Table II), which had been in my possession for only one day before this feeding experiment began On both September 6 and 7 the feces of this duck were examined for strigeid eggs, but none were found On September 10, however, more than two hundred strigeid eggs were collected from the feces On the evening of September 10 the duck was killed and more than two hundred mature Cotylurus were obtained from its intestine Careful study showed that these parasites agreed in all respects with those obtained as a result of my other feeding experiments in which I used naturally infested snails Therefore, I conclude that all the strigeid parasites obtained from my experiments must have developed from *Cercaria douglasi* Cort, 1917

The life-cycle — Cort and Brooks (1928, p 191) obtained *Cercaria douglasi* from *Physa sayii oneida* Baker, *Physa parkeri* "Currier" De Camp, *Lymnea emarginata angulata* Sowerby, *L stagnalis appressa* Say and *L stagnalis perampla* Walker This list, therefore, also indicates certain snails into which the miracidia of this species penetrate Moreover, I have collected the eggs of this species and observed the development of the miracidia within the eggs Hence all the salient stages of the life-history of *C flabelliformis* have been seen and the hosts of a complete life-history are known My observations on this species and on the life-cycle of another species of Cotylurus which has been experimentally determined (Van Haitsma, 1930), together with the data of Mathias (1925, p 63) on *S tarda*, permit me to outline briefly the life-cycle of *C flabelliformis* In a general way this outline will probably apply to all species of Strigeidae except that in most species the second intermediate host is a vertebrate The periods of time suggested in this outline imply summer temperatures

Stage of Development	*Time Required*
Egg develops into miracidium	about 3 **weeks**
Miracidium swims in the water and penetrates into first snail host	a few hours
Miracidium metamorphoses into mother sporocyst, which gives rise to secondary sporocysts that produce cercariae	about **6 weeks (Mathias)**
Cercariae escape into water and penetrate into second snail host	within 1 day
Cercariae develop into tetracotyles within second snail host	about 6 **weeks**
Second snail host ingested by a duck in which tetracotyles develop into egg laying adults	**3 or 4 days**
Egg laying stage within the duck	**about 1 week**

It is possible, therefore, under favorable conditions for the whole life-cycle to be completed within four months, but during the winter the process of development doubtless continues at a much slower rate and may even come to a standstill Eggs which were kept at low temperatures for three weeks did not develop noticeably, but when the temperature was raised to 23° C development again proceeded Cercariae also become less active as the temperature decreases, yet the temperature requirement for the penetration of strigeid cercariae into the second intermediate host is considerably less than that of schistosome cercariae There is good reason to believe that the tetracotyles pass the winter within the snail host, since they may be found in large numbers in the snails in early summer As already explained, the stage within the final host attains sexual maturity very soon and lives only a short time The periods suggested for the adult in the outline above are doubtless too short for many other Strigeidae

The life-cycle of *C flabelliformis*, as far as studied, is closely similar to that of *S tarda* The stages within the first snail host were not actually studied by me, but doubtless these two species are also similar with respect to this part of the life-cycle Hence the description of these stages in the outline above was confidently paraphrased from Mathias' description of *S tarda* In a species of Diplostomum, syn Proalaria, and another species of Cotylurus, the period from the penetration of the miracidia to the appearance of the cercariae was also about six weeks

The determination of this life-cycle corroborates the fact developed since 1920 (La Rue, 1926, pp 269 271) that the Strigeidae are not metastatic, as was supposed from 1889 until 1920 In the strigeid life-cycle there is an alternation of generations as well as an alternation of hosts While the number of eggs produced by the hermaphroditic adult is comparatively small, the multiplication within the first snail host is enormous Under favorable conditions a few infested ducks remaining on a lake for a few days may during the period of the life-cycle of the present species infest the snails of the lake with millions of tetracotyles In this way this species and others of the family Strigeidae are well adapted for distribution by migratory birds, which may remain on one body of water for only a short time

Experiments with chicks — During the summer (1928) following that in which the life-history of this species was determined, attempts were made to develop tetracotyles in chicks Two chicks, only two weeks old at the beginning of the experiment, were fed from twenty to fifty tetracotyles a day from June 29 to July 7 The tetracotyles taken from the snails were placed on moistened bread and fed in this way Fecal examinations, both before and after this experiment, showed that no eggs were present On July 7 one of the chicks was killed and examined Its intestines were free from parasites Experimental feeding of the other chick was discontinued till it was about seven weeks old Beginning on August 3 crushed snails, thirty-six in all, were fed to this chick during three days On August 7 a fecal examination revealed the presence of strigeid eggs On August 8 the chick was killed and examined Its intestines contained about fifty mature and nearly mature *C flabelliformis* similar in all respects to those obtained from my experimental ducks This experiment demonstrates, therefore, that in chicks of the proper age the parasite develops to maturity just as readily as in domestic ducks

TRANSIT DEVELOPMENT

Three characteristics of *C flabelliformis* deserve special attention, since they have a bearing upon the interpretation of its life-cycle These are of small size, early sexual maturity and short life Mature specimens are smaller than those of all other known species of the former genus Strigea, being noticeably smaller than *S tarda* as described by Lühe (1909, p 163) and Mathias (1925, p 25) Associated with its small size is an early sexual maturity In my experiments I, II, III and XI, and in the experiment with the chick, numerous eggs were found in the feces on the fourth day after the first experimental feeding Mathias (1925, p 24) found some eggs of *S tarda* in the feces of his experimental ducks on the third day after infestation, but Lutz (1920, pp 128-129) states that the species which he hastily supposed to be *S tarda* required about ten days after infestation to attain the egg-laying stage The small size and early sexual maturity of *C flabelliformis* are probably physiologically correlated with its short life In several of my experiments this species remained in the ducks a much shorter time than the monostomes and echinostomes which were also present Lutz (1920, p 128) predicted that some of the smaller holostomes (Strigeidae) would prove to remain in their definitive hosts only a short time Mathias (1925, p 64) found that a mass infestation of *S tarda* in domestic ducks did not last more than twelve to eighteen days In my experiment VII the parasites left the duck within eleven days after the last experimental feeding Now all three of these characteristics of the adult *C flabelliformis*, small size, early sexual maturity and short life, are also characteristic of cases of transit development in the sense that this term was employed by Faust and Nishigori (1926, p 94) It is pertinent, therefore, to inquire whether the development of *C flabelliformis* in the domestic duck represents a case of transit development

Before attempting to answer this question, it is desirable to consider the percentage of tetracotyles which develop into adults in domestic ducks and also the lack of host specificity of *C flabelliformis* and *S tarda* According to a previously discussed estimate, less than two per cent of the tetracotyles fed to the domestic duck succeed in developing to the egg-laying stage Although the percentage of viability is not known and definite records of the percentage of tetracotyles of other species of strigeids which develop to the egg-laying stage in their definitive hosts are not available, yet my experience in more than twenty successful feeding experiments involving five species of holostomes leads me to believe that the percentage of tetracotyles of the present species which develop into egg-laying adults in the domestic duck is extraordinarily small Other conditions being equal, a low percentage of development of tetracotyles in the definitive host indicates a lack of adaptation between parasite and host Such a lack of adaptation is favorable to the interpretation of transit development

There are also several phenomena indicating a lack of host specificity of *C flabelliformis* and *S tarda* which are significant of transit development Cort and Brooks (1928, p 191), after naming the different kinds of snails from which they obtained the cercaria of *C flabelliformis*, declare that "the lack of specificity displayed by this species in its development in so many different hosts we believe goes beyond anything yet reported for holostome cercariae" To this declaration may be added that the lack of specificity of the cercaria is matched by that of the tetracotyle, which also has been found in five species of snails belonging to two genera Doubtless the list of hosts of the cercariae and metacercariae of this species is not yet complete So far, the adult *C flabelliformis* has been found in seven species of ducks belonging to five genera and it has been experimentally developed in a chicken, but if its similarity to *S tarda* includes also a similar diversity of definitive hosts, we may expect to find it in a much greater variety of hosts By experimental feeding Mathias (1925, p 32) obtained a complete development of *S tarda* in both domestic and wild ducks and also in a quail Hence it seems probable that the present species, which closely resembles *S tarda* in its life-history, may be found in more kinds of hosts If among these hosts there should be found one in which a greater percentage of tetracotyles would develop to sexual maturity, grow more slowly and to a larger size, and live longer, there would be sufficient evidence to conclude that the development of *C flabelliformis* in ducks is a case of transit development, but as long as such evidence is lacking it can only be said that the development of this species in domestic ducks resembles cases of transit development

Pathology in the snail — The life-history experiments described above demonstrate clearly that snails heavily infested with the cercariae of *C flabelliformis* may be killed by the developing tetracotyles Of the snails experimentally infested by Professor Cort, fifty per cent died before the tetracotyles were fully developed, while other snails, not experimentally infested and kept under similar or even less favorable conditions, showed a comparatively low death-rate Faust (1920, pp 1–16) has made a careful study of pathological conditions resulting from the development of sporocysts and cercariae in snails If similar pathological conditions are produced by developing tetracotyles, they would readily account for the high death-rate of heavily infested snails

Pathological symptoms in the ducks — Several symptoms of disease were observed in my experimental ducks and during the course of the experiments four of the nine heavily infested ones died These symptoms may be summarized as follows (*a*) paresis indicated by a leg weakness and extraordinary tendency to sit, (*b*) muscular incoordination, resulting in inability to direct locomotion, (*c*) nervous twitchings of the head and wings, (*d*) dyspnea, indicated by a labored expansion and contraction of the body, (*e*) diarrhea and (*f*) irregular appetite Two apparently healthy ducks which were given extraordinarily heavy feedings of snails containing tetracotyles suddenly died within a week without showing definite symptoms My observations of symptoms are confirmed by similar observations of Katsurada (1914, p 310), Galli-Valerio (1914, pp 97–115) and Tabangui (1926, p 5) in helminth infestations

Although it seems probable, therefore, that at least some of the symptoms of disease in my young ducks were due to the parasitic infestations, it is also not improbable that some of the symptoms observed were due to cold and dampness or to improper feeding Equally severe infestations did not always produce the same symptoms in ducks of the same age Besides, control experiments for the definite purpose of relating the symptoms of disease to the parasites were not performed Moreover, Dr Ernest Hartman discovered a species of Leucocytozoon in some of my ducks This double infestation makes the problem of explaining the symptoms twice as complicated, especially so since the pathological effects of Leucocytozoön on the domestic duck is not known (Wenyon, 1926, p 908)

Although it is impossible at present to attribute definitely any symptom of disease in my ducks to *C flabelliformis*, my observations suggest the opinion that well-directed and controlled experiments on large numbers of ducks will demonstrate that there is a connection between some of the symptoms observed and the parasitic infestations Mathias held the opposite opinion, but probably he did not observe very heavy infestations As has already been described (Part I, above), *C flabelliformis* digests away the columnar epithelium of the intestinal mucosa of its host and causes a congestion of blood in the subepithelial connective tissue of the host's mucous membrane at the points of attachment of the parasites Consequently, it seems reasonable to believe that large numbers of the parasites should have injurious effects upon their hosts It also seems plausible that the irritations of the intestinal wall of the duck by the parasites, or possibly by their toxic secretions, should cause some of the nervous symptoms observed

Summary – The life-cycle of *C flabelliformis*, here described, is the first strigeid life-cycle to be determined in North America The cercaria has previously been described by Cort and Brooks (1928) and the metacercaria by Hughes (1929) The adult is described in Part I of the present paper It is noteworthy that these stages of development were all secured from the same kinds of snails, from the same lake, during the same summer The peculiarities of this life-cycle which suggested that it may be a case of transit development are discussed, and the pathological effects that this parasite has or may have upon its hosts are considered

ACKNOWLEDGMENTS

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GRAND RAPIDS, MICHIGAN

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EXPLANATION OF PLATES XLI–XLII

All the figures except 11 and 12 are drawn according to the same scale indicated by the reference line near Figure 10 The magnification of Figures 11 and 12 is indicated by the reference line near Figure 12 Both reference lines represent 0 1 mm

ABBREVIATIONS

ac acetabulum
ag — adhesive gland
alhf anterior lobe of the holdfast organ
apex — antero posterior excretory vessel
bc — bursa copulatrix
cvd — common vitelline duct
dex — dorsal excretory vessel
eg — egg
ejd — ejaculatory duct
eso — esophagus
exp — excretory pore
exs — excretory space
ga genital atrium
hb hindbody
int intestinal cecum
lc — Laurer's canal
lsc — lateral sucking cup
lvd left vitelline duct
mdex — median dorsal excretory vessel
mdvex — median dorso-ventral vessel
mg Mehlis gland
mvex — median ventral excretory vessel
n — nerve strands
ofb — opening of forebody
oot ootype
os oral sucker
ov ovary
ovd — oviduct
pbc — primordium of bursa copulatrix
ph — pharynx
plhf — posterior lobe of holdfast organ
sv — seminal vesicle
t_1 — anterior testis
t_2 — posterior testis
tex transverse excretory vessel
ut — uterus
uta ascending limb of the uterus
utd — descending limb of the uterus
vd vas deferens
ve_1 vas efferens of t_1
ve_2 — vas efferens of t_2
vex ventral excretory vessel
vit vitellaria
vr vitelline reservoir

PLATE XLI

FIG 1 Reconstruction of female genital system Left view The vitelline reservoir lies on the left of Mehlis gland

FIG 2 Reconstruction of the male genital system Left view The vas deferens lies between the two vasa efferentia

FIGS 3 9 Posterior views of a consecutive series of cross-sections of an early developmental stage of an adult Of this series Figure 9 represents the foremost section, cut in the region between the two testes Figures 3 5 show the bursa copulatrix still in the primordial stage, in them the ventral excretory vessels can be traced forward from the excretory pore In Figure 6 branches from the ventral excretory vessels extend between the primordium of the bursa copulatrix and the posterior testis to form the ventral excretory vessels. In Figures 7–9 the ventral excretory vessels are separated from the dorsal vessels by the posterior testis, and the dorsal vessels anastomose with subcuticular excretory spaces Figures 4–9 also show the vitellaria to be in two fields in this early adult stage of development

FIG 10 Diagramatic reconstruction, left side view showing digestive and excretory systems and the distribution of vitellaria The peripheral excretory spaces are not represented

FIGS 11–12 The external appearance of *C flabelliformis* showing the variability of the forebody

PLATE XLII

FIGS 13 16 A consecutive antero-posterior series of reconstructions representing thick cross-sections of the forebody as seen in anterior view

FIG 13 The forebody looking into the cup showing the two lappets of the posterior lobe of the holdfast organ

FIG 14 Reconstruction of sections between the pharynx and acetabulum The intestinal ceca diverge anterior to the acetabulum

FIG 15 Region of the acetabulum, showing both lobes of the holdfast organ lateral sucking cups and more conspicuous excretory vessels and spaces

FIG 16 Region of the adhesive gland The intestinal ceca bend ventrad The dorsal and median dorso-ventral excretory vessels are represented

FIG 17 Reconstruction of somewhat oblique sections through the dorsal wall of the forebody, showing the relative positions of the digestive, excretory and nervous systems in this body region

FIG 18 Reconstruction of cross-sections of the hindbody anterior to the ovary Anterior view The ventral excretory vessels are united by the transverse vessel The intestinal ceca bend ventrad The vitellaria are distributed throughout almost the entire section

FIG 19 Reconstruction of the middle region of the hindbody Anterior view Ovary and anterior testis not shown The median dorsal excretory vessel divides to form the two dorsal vessels The relative positions of the oviduct Laurer s canal, common vitelline reservoir vas deferens, descending limb of the uterus, and ventral excretory vessels are indicated The vitellaria are restricted to the ventral half of the section

FIG 20 Reconstruction of the region behind the posterior testis Anterior view, showing relative position of seminal vesicle, ejaculatory pouch and duct, descending uterus and ventral excretory vessels anastomosing with subcuticular excretory spaces Three lobes of the posterior testis are also shown

PLATE XII

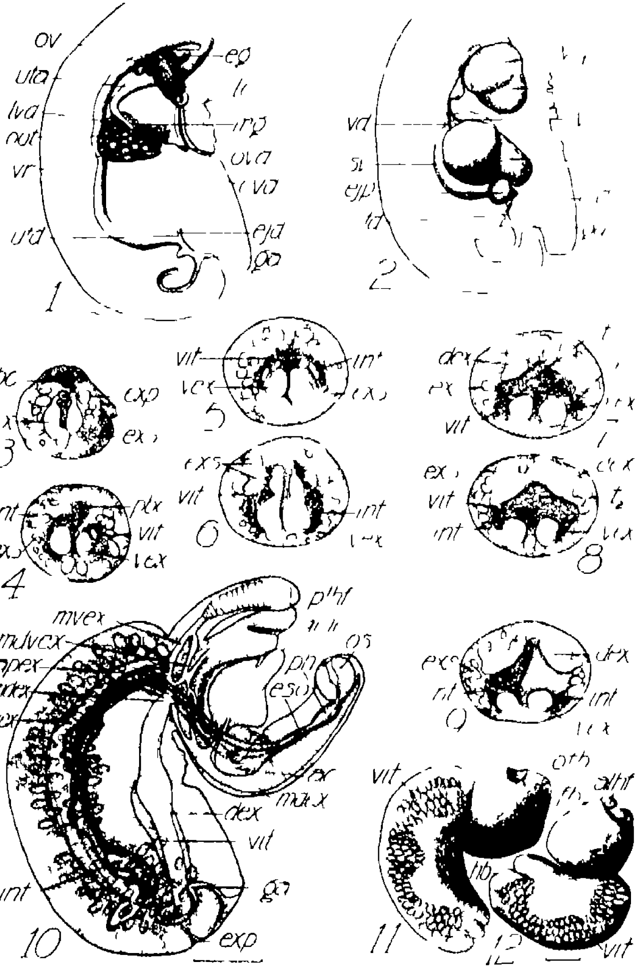
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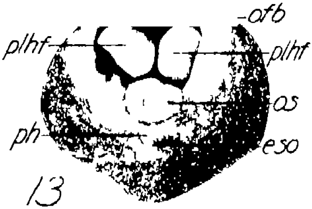
PLATE XIII



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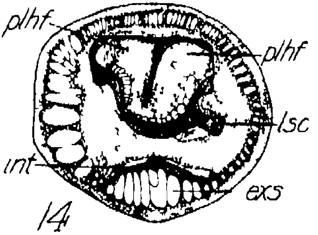

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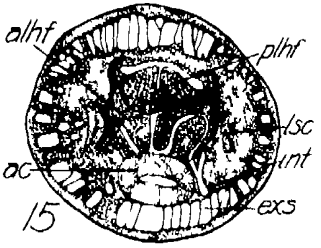

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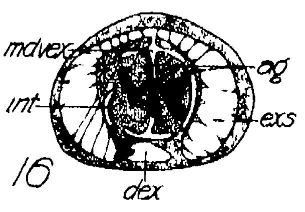

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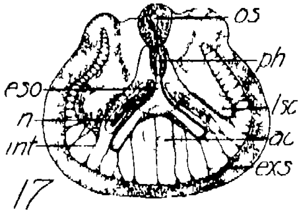

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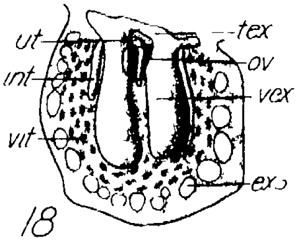

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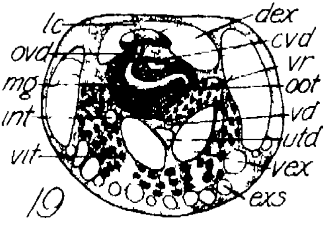

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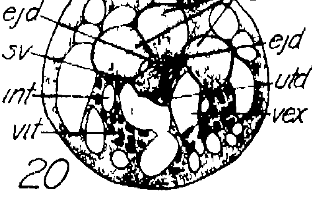

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STUDIES ON THE TREMATODE FAMILY STRIGEIDAE (HOLOSTOMIDAE) NO XXIII *DIPLOSTOMUM FLEXICAUDUM* (CORT & BROOKS) AND STAGES IN ITS LIFE-HISTORY *

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THE new adult trematode of the family Strigeidae, here described, was obtained as a result of infestation experiments made during the summer of 1927, the life-cycle of this species was experimentally traced during the autumn of the same year Since, in the course of these experiments, it was shown that the adult develops from *Cercaria flexicauda* Cort & Brooks (1928, pp 183–186), the name of the present species becomes *Diplostomum flexicaudum* (Cort & Brooks)

The use of the generic name Diplostomum for this species requires an explanation The genus Diplostomum was erected by von Nordmann (1832) for certain larval trematodes found in the eyes of certain European fish The first of these species he described as *Diplostomum volvens* He erroneously believed his specimens to be adult and gave a detailed description of them accompanied by excellent figures Later the Ehrhardt brothers, by means of feeding experiments reported by Braun (1894, pp 156–167), demonstrated that *D volvens* developed within the laughing gull, *Larus ridibundus*, into *Hemistomum spathaceum* (Rud) Thus it was shown that the genus Hemistomum Dies , 1850, was in part, at least, a synonym of Diplostomum von Nordmann, 1832 Krause (1915, p 233) showed that Hemistomum

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* Contribution from the Biological Laboratory of Calvin College and from the Biological Station and the Zoölogical Laboratory of the University of Michigan. This is the twenty-third of a series of studies on the family Strigeidae by Professor George R, La Rue, his students and associates.

Dies is a synonym of Alaria Schrank, 1788 Moreover, according to Stiles and Hassall (1912, pp 88, 281 [*Index Catalog*]), the type of Hemistomum Dies, by inclusion and also by first species rule, is *alatum* = *Alaria vulpis* By reason of this fact the name Hemistomum Dies is a synonym of Alaria Schrank, and therefore is not available for those members of the genus Hemistomum, 1850, which are non-congeneric with *Alaria alata* The adult developed from *Diplostomum volvens* does not belong in the genus Alaria, therefore the name Diplostomum becomes available according to the rules of priority as the generic name for *D volvens* *Spathaceum* (Rudolphi, 1819), however, has priority over *volvens* (von Nordmann, 1832) Hence the correct name of von Nordmann's species becomes *Diplostomum spathaceum* (Rud) Since the present species is congeneric with *D spathaceum*, it is placed in the genus Diplostomum von Nordmann, 1832 Diplostomum Brandes, 1888, falls as a homonym, but the group name Diplostomulum Brandes, 1892, for the metacercariae continues to be available

PART I THE ADULT WORM

Diplostomum flexicaudum (Cort & Brooks) closely resembles two other recently described species of Diplostomum It is very similar in structure to *D spathaceum* (Rud), described by Krause (1915, pp 136–147), and its similarity to *D huronense* (La Rue), described by La Rue (1926, pp 26–35), is only slightly less pronounced All three of these species inhabit the intestines of gulls Moreover, *D flexicaudum* and *D huronense* were obtained from the same species of gulls of the same region, Douglas Lake Therefore my findings on *D flexicaudum* are compared in detail with the descriptions of *D spathaceum* and *D huronense* referred to above

SPECIFIC DIAGNOSIS

Diplostomum flexicaudum (Cort & Brooks) — Fixed material, adults Characters of the genus, forebody, concave ventrally, 1 0–1 4 × 0 5–0 7 mm, not set off from the hindbody by a deep groove, hindbody, cylindrical to club-shaped, usually narrower anteriorly, 1 3–1 9 × 0 37–0 55 mm, oral sucker, 0 065–0 08 ×

0 06–0 085 mm , but smaller than the acetabulum, 0 06 0 09 × 0 06–0 135 mm , the latter circular to transversely elliptical, often covered by the mushroom-shaped holdfast organ, ovary, ellipsoidal, 0 09–0 135 × 0 09–0 16 × 0 13–0 2 mm , testes horseshoe-shaped, in the posterior half of the hindbody, uterus forming a large coil between the testes, vasa efferentia unite into vas deferens on the anterior surface of the first testis, eggs, 0 09 0 115 × 0 057 0 07 mm , habitat, intestines of herring-gulls at Douglas Lake, Michigan Metacercaria of *Diplostomum flexicaudum* (Cort & Brooks) = *Diplostomulum gigas* Hughes & Berkhout, 1929 habitat, crystalline lenses of the eyes of common suckers of Douglas Lake Cercaria of *D flexicaudum* = *Cercaria flexicauda* Cort & Brooks, 1928

External features —The external appearance of *D flexicaudum*, *D spathaceum* and *D huronense* is so similar that the following description of *D flexicaudum* applies equally well to the other two species Each animal consists of a ventrally concave forebody, oval in outline, and a more or less curved, club-shaped to cylindrical hindbody (Fig 1) The anterior end of the forebody is often made irregular by two processes, which extend variably forward on either side of the slightly protruding oral sucker In other specimens depressions were found at the sides of the oral sucker instead of processes, or a depression may be found on one side and a process on the other in the same specimen The posterior and lateral margins of the forebody are usually inturned ventrally The transversely elliptical acetabulum is located near the middle of the ventral surface of the forebody Behind the acetabulum and often partly covering it is the holdfast organ, mushroom-shaped when extended and usually provided with a more or less deep longitudinal groove on its ventral surface In the retracted condition the holdfast organ forms a deep cavity extending dorsad and posterad Owing to its different states of contraction, the dimensions of the holdfast organ differ so greatly that measurements can have no taxonomic significance The hindbody arises from the posterior dorsal surface of the forebody The two body regions may be more or less flexed dorsad at their junction, or they may lie in a nearly straight line On the dorsal side near the posterior end of the hindbody the circular to elliptical opening of the bursa copulatrix is readily seen

Measurements — In Table I dimensions of the body regions and of some of the more regularly shaped organs of *D flexicaudum* are compared with corresponding measurements of *D spathaceum* and *D huronense* made by Krause and La Rue, respectively In this table Krause's and La Rue's measurements have a much wider range than my own, probably because my measurements were based on a smaller number of specimens, all of which appeared to be full-grown and moderately extended This may also explain why the mean of my measurements approaches the larger dimensions presented by Krause If Krause had also recorded the mean of his measurements, it would have greatly facilitated a comparison of the three species From the present data it appears that all three species are nearly equal in their dimensions The most notable differences between *D flexicaudum* and *D spathaceum* are that *D flexicaudum* has a somewhat larger ovary and that its eggs are variable in dimensions

Table I indicates more distinct differences between *D flexicaudum* and *D huronense* The measurements of the forebody, oral sucker and acetabulum of *D huronense* are larger than my corresponding measurements of *D flexicaudum*, and the hindbody of *D huronense* is shorter and thicker, but its pharynx is narrower The distinctness of these two species morphologically agrees with results which I have obtained from feeding experiments *D flexicaudum* was developed from metacercariae found within the lens capsule of the eye of the common sucker, *Catostomus commersonnii* (Lacépède), *D huronense* was developed from smaller metacercariae found in the vitreous humor of the eye of the trout perch, *Percopsis omiscomaycus* (Walb) Hughes and Berkhout (1929, pp 483–494) have described these two metacercariae and pointed out the differences between them

Organs of attachment — These organs include the oral sucker, the ear-like lappets or sucker-like depressions at the sides of the oral sucker, the acetabulum, the holdfast organ and the ventrally inturned margins of the forebody For a description of these organs and an explanation of the sources of the granular secretion

TABLE I COMPARATIVE MEASUREMENTS OF *D flexicaudum* (CORT & BROOKS) AND SIMILAR SPECIES

Items	*Diplostomum flexicaudum*			*D spathaceum*	*D huronense*	
	Number measured	Range	Mean	Krause s measurements	La Rue s measurements	Mean of La Rue s measurements
Forebody						
Length	13	1 0–1 4 *	1 16	0 60–1 27	0 518–1 33	0 956
Breadth	13	0 5–0 7	0 61	0 36–0 69	0 503–0 873	0 715
Hindbody						
Length	13	1 3–1 9	1 65	0 77–2 1	0 518–1 332	1 038
Breadth	13	0 37–0 55	0 44	0 23–0 71	0 407–0 592	0 490
Oral sucker						
Length	10	0 065–0 08	0 072	0 054–0 094	0 090–0 112	0 099
Breadth	16	0 06–0 085	0 069	0 054–0 099	0 051–0 105	0 079
Pharynx						
Length	10	0 07–0 09	0 077	0 041–0 081	0 075–0 098	0 083
Breadth	6	0 04–0 06	0 05	0 036–0 072	0 036–0 061	0 048
Acetabulum						
Antero-posterior	16	0 06–0 09	0 076	0 054–0 11	0 060–0 12	0 085
Breadth	16	0 06–0 135	0 09	0 059–0 14	0 097–0 138	0 111
Ovary						
Antero-posterior	10	0 09–0 135	0 109	0 077–0 13	0 069–0 148	0 120
Dorso-ventral	10	0 09–0 16	0 121	0 099–0 12		
Breadth	10	0 13–0 2	0 165	0 10–0 17	0 123–0 181	0 166
Egg						
Length	14	0 09–0 115	0 101	0 108	0 095–0 105	0 104
Breadth	14	0 057–0 07	0 062	0 063	0 053–0 060	0 057

* All measurements are given in millimeters Measurements of the body regions were made upon unmounted specimens Length was measured along the median line of the respective body regions as seen in ventral view The breadth measurements represent maximum dimensions as seen in frontal aspect The measurements of the length of the forebody include the lateral lappets when they were extended The breadth measurements of the ovary and acetabulum are only approximations They represent the products of the thickness of the sagittal sections multiplied by their number My egg measurements were obtained from eggs collected from the feces of the gulls The egg measurements of *D huronense* were made upon uterine eggs (La Rue 1926 p 30)

in the tips of the ear-like lappets or sucker-like depressions reference may be made to Krause's description (1915, pp 106–111) of *D spathaceum* My observations have yielded additional information concerning the functions of these organs According to these observations the chief organs of attachment of these parasites are the extended ear-like lappets at the sides of the oral sucker In a portion of the host intestine, fixed in corrosive-acetic, the parasites were attached only by means of the extended ear-like appendages or lappets which had been pressed into the tissues of the host In two specimens which had been shaken free from the host finely granular globules, lightly stained with hematoxylin, were found on the secreting surfaces of the lappets These globules appeared to be mucilaginous Their presence suggested that the parasites were attached by means of this substance rather than by any mechanical action of the lappets This explanation agrees with that of von Linstow (1877, pp 187–198), who called the secreting glands "*Leimdrüsen*" The columnar epithelium of the host intestine had been completely removed, presumably owing to the post-mortem digestive action of the host, since the denuded area extended beyond the range of the parasites Consequently, the parasites were attached to the subepithelial connective tissue of the host In attached parasites, which had been killed and fixed *in situ*, the oral sucker, acetabulum and holdfast organ gaped widely open, but they were not in contact with the tissues of the host Their gaping condition indicated that the parasites had released their hold before they died In some specimens shaken free from the host the acetabulum protruded almost entirely beyond the ventral surface of the forebody It is probable that the oral sucker, acetabulum, holdfast organ and the ventrally inturned margins of the forebody cooperate with the ear-like lappets of the living parasites in the process of attachment It also seems probable that the lappets and acetabulum are contracted in life so as to hold the ventral surface of the parasite closely against the intestinal wall of the host In the holdfast organ glandular tissue continuous with that of the so-called adhesive gland extended to the ventral surface Presumably the secretion of these glands is conveyed into the cavity of the holdfast organ, where it may perform a function, possibly digestive In the present material, however, the only basis for this belief is to be found in the position of the glandular cells The intestinal wall of the host did not reveal serious pathological disturbances which could be ascribed to the presence of the parasites

Digestive system — This system of organs of *D flexicaudum* (Fig 1) resembles that found in other diplostomes On being shown some sections of this parasite, Dr William McKay German, pathologist at Blodgett Hospital, Grand Rapids, Michigan, recognized a brownish pigment in the digestive ceca which he interpreted to indicate old blood From this it appears that this parasite fed upon the blood of its host Disintegrating nuclei were also present in the digestive ceca Injuries to the host tissue which might explain the source of the blood were not observed

Amphitypy — Krause described *D spathaceum* as amphitypic A similar condition was found in *D flexicaudum* The ovary and Mehlis' gland may be found in the right side of some specimens and in the left in others This reversal of position of these organs is accompanied by a reversal of position of the other organs which do not lie in the median plane and are not bilaterally symmetrical, particularly the ascending limb of the uterus and the vasa efferentia

Male reproductive system — The testes of *D flexicaudum* (Fig 2) are roughly horseshoe-shaped They lie in the posterior half of the hindbody The vasa efferentia arise from the anterior median ventral surfaces of the testes and unite with the vas deferens in front of the first testis (Figs 2, 5) The vas deferens bends toward the median ventral line and enlarges behind the posterior testis to form the seminal vesicle The seminal vesicle coils vertically, first extending dorsad and posterad to the genital atrium and then bending anterad to the posterior testis (Figs 3-4), where its diameter diminishes and its wall becomes thickly muscular to form the ejaculatory duct The ejaculatory duct extends dorsad and posterad to the genital atrium into which it opens dorsal to the opening of the uterus The position of the testes and male genital ducts of *D flexicaudum* agrees in detail with that given in Krause's description of these organs in *D spathaceum*, but in *D huronense* the testes are located relatively farther forward (La Rue, 1926, p 31, and Fig 1)

Female genital organs — From the posterior dorsal side of the ellipsoidal ovary the oviduct extends dorsad and posterad along the dorsal side of the anterior testis to the right or the left of the median line to Mehlis' gland (Fig 10) A short distance from the ovary the oviduct is slightly enlarged (Fig 8), but this enlargement is not so definite as Krause's (1915) figure N indicates for *D spathaceum* From this enlargement Laurer's canal arises and extends to its opening near the median dorsal line of the hindbody As the oviduct enters Mehlis' gland the common vitelline duct empties into it (Fig 6) Closely behind the junction of these two ducts the ootype bends to the right, or to the left, and becomes the ascending limb of the uterus, which begins its "ascent" anterad by forming a large spiral coil between the testes (Fig 9) Thence the ascending uterus extends anterad along that side of the body containing Mehlis' gland, over the ovary (Fig 7), to a point somewhat beyond one half of the distance between the ovary and the anterior end of the hindbody (Fig 10) Here it bends and becomes the descending uterus, which extends along the midventral line ventral to the vas deferens to the genital atrium The course of the female genital ducts, here described, agrees in detail with that of *D spathaceum* described by Krause (1915, text fig N), except that in *D flexicaudum* the coil of the ascending uterus between the testes is more extensive The oviduct of *D flexicaudum* near its junction with Laurer's canal is less coiled than the corresponding part of the oviduct of *D huronense* as described by La Rue (1926, Fig 4)

The vitelline system is closely similar in *D flexicaudum*, *D spathaceum* and *D huronense* In each of these species the vitellaria extend from a position somewhat anterior to the acetabulum to the posterior end of the hindbody In the region of the testes of all three species the vitellaria form only a narrow midventral strip The points of entrance of the right and left vitelline ducts into the intertesticular vitelline reservoir shown in my Figure 6 is an individual characteristic In most specimens of *D flexicaudum* the right and left vitelline ducts empty into the ventral end of the vitelline reservoir

The excretory system -- My findings on the excretory system of *D flexicaudum* agree quite closely with those described by Krause (1915, pp 145–146) for *D spathaceum*, but in the light of my previous studies on the excretory systems of *Crassiphiala bulboglossa* Van Haitsma (1925, p 124) and of *Cotylurus flabelliformis* (Faust) (Van Haitsma, 1931), my interpretation of the excretory vessels of *D flexicaudum* is somewhat different

The excretory system can be traced most easily by means of cross-sections of an early developmental stage of the adult (Figs 11 19) The common excretory duct, opening at the excretory pore posterior to the opening of the bursa copulatrix, is short, its length being equal to the thickness of the body wall (Fig 19) The common excretory duct divides into two branches, which extend ventrad along either side of the bend of the descending limb of the uterus near its posterior end (Fig 19) Near the ventral side of the body these two branches bend anterad and continue along either side of the descending limb of the uterus throughout its length (Figs 14 19) These right and left ventral excretory ducts are the "Uterusgefasse" of Krause In front of the anterior bend of the uterus they unite into a large median ventral vessel which extends to the posterior part of the forebody (Fig 13), where it anastomoses with numerous small excretory canals found in the ventral lip of the forebody These canals continue anterad in the lateral regions of the forebody (Figs 11–12)

From the dorsal region of each of the two branches of the common excretory duct (Figs 18 19) a dorsal vessel arches around the side of the bursa copulatrix and opens into wide peripheral excretory spaces of the dorsal region and sides of the posterior half of the hindbody (Figs 16–17) For this reason the right and left dorsal vessels of this region of the hindbody are not distinguishable from the peripheral excretory spaces In the region of Laurer's canal the right and left dorsal vessels again appear distinctly (Fig 15), and at a short distance in front of this canal they unite into a median dorsal vessel that extends to the anterior end of the hindbody (Fig 14) Immediately behind the adhesive gland at the junction of forebody and hindbody the median dorsal and median ventral vessels unite into a vessel that connects with numerous small canals in the ventral lip of the forebody, as already explained (Fig 13)

In the forebody there are, in addition to a median vessel, three *lateral vessels on each side* *One of them lies dorsal to the digestive* cecum, another is found near the nerve strand, the outermost one is located near the margin of the forebody (Figs 11-12) These lateral vessels of the forebody are small and sometimes difficult to distinguish in preserved specimens At the level of the pharynx they form on each side a close network which anastomoses with the median vessel The median vessel extends posterad to the region dorsal to the holdfast organ (Figs 11 12), where it is dilated Behind the holdfast organ it is connected with the lateral vessels by means of transverse vessels (Fig 13) It appears probable that the median vessel of the forebody is also connected by means of small indistinct canals with the median dorsal vessel of the hindbody

This interpretation of the excretory system of *D flexicaudum* is in complete accord with my findings on the excretory systems of *Crassiphiala bulboglossa* Van Haitsma (1925) and *Cotylurus flabelliformis* (Faust) (Van Haitsma, 1931) as far as they were traced, except that the dorsal vessels of the posterior half of the hindbody of *D flexicaudum* are indistinct, owing to their anastomoses with peripheral excretory spaces Although several previous investigators (Brandes, 1890, pp 568-570, Poirier, 1886, Guberlet, 1922) have recognized only two main excretory vessels in the hindbodies of this group of parasites, it is believed that the interpretation of the excretory system of the hindbody here presented will be found applicable to the excretory systems of the hindbodies of all adult Strigeidae

Pathological symptoms in the definitive hosts — As explained above, no pathological effects of the parasites were observed in the tissues of the hosts, but there were indications that the parasites fed upon the blood of the host Heavy infestations appeared to retard the growth of the gulls and to keep them in an emaciated condition even though they were well fed. Weakness and nervousness were also indicated by the movements of the wings of the birds. In birds heavily infested the wings drooped repeatedly, only to be drawn back spasmodically. Such movements were continually observed in my gulls for about two weeks before they were killed. It can only be conjectured whether the movements were caused by secretions of the parasites or by the mechanical irritation of the parasites upon the intestinal wall of the host. These pathological symptoms are similar to some observed by Van Haitsma (1931) in domestic ducks heavily infested with *Cotylurus flabelliformis* (Faust).

Comparison of D. flexicaudum and D. spathaceum.—Owing to the close resemblance in structure and life-history between *D. flexicaudum* and *D. spathaceum*, as the latter was described by Krause (1915) and Szidat (1924), it is desirable to summarize the differences between them. The dimensions of the eggs of *D. flexicaudum* are 0.09-0.115 × 0.57 0.07 mm. According to Krause, the measurements of the eggs of *D. spathaceum* are invariably 0.108 × 0.063 mm. According to evidence which will be presented in a later article, the miracidium of *D. flexicaudum* was experimentally developed in *Lymnea emarginata angulata*, but, according to Szidat, the miracidium of *D. spathaceum* develops in *L. stagnalis*, *L. palustris* O. F. Müll. and *L. ovata* Drap. The cercaria of *D. flexicaudum* assumes a characteristic resting position in the water. With the tail furcae outspread upwardly and with the tail-stem bent, the body hangs in the water in a nearly horizontal position. Szidat (1924, p. 251, and Fig. 1) describes a different resting position for the cercaria of *D. spathaceum*. I found the diplostomula of *D. flexicaudum* in the lenses of the eyes of common suckers of North America, Szidat found the diplostomula of *D. spathaceum* in the eyes of *Acerina cernua* and *Leuciscus rutilus*, and von Nordmann found it in the vitreous humor and the lens of *Perca fluviatilis* and the burbot (*Gadus lota*), all in Europe. The adults of these two species also differ in several minor ways. In *D. flexicaudum* the pharynx averages slightly longer than the oral sucker and it is almost as wide. According to Krause, the pharynx of *D. spathaceum* is nearly always shorter than the oral sucker and less than three fourths as wide In *D spathaceum* the acetabulum is seldom covered by the holdfast organ, but according to my findings this is often the case in *D flexicaudum* It also appears from my measurements of Table I that the ovary of *D flexicaudum* is somewhat larger in proportion to the size of the body than the ovary of *D spathaceum* Then, too, the coils of the uterus between the testes appear to be larger in *D flexicaudum* than in *D spathaceum* In view of all these differences it appears that *D flexicaudum* and *D spathaceum* are distinct species, but, owing to the many close similarities between them, it is desirable that a careful comparison of their structure and life-histories should be made to prove that the differences which I have found are not due to differences in observation In this connection it is of interest that common terns banded in America have later been found in Europe

PART II LIFE-HISTORY

The life-history of *Diplostomum flexicaudum* (Cort & Brooks) was the third American strigeid life-cycle to be determined during the summer and autumn of 1927 Infestation experiments here described have demonstrated that the adult of this species developed from *Diplostomulum gigas* Hughes & Berkhout (1929, pp 483 488) and that this metacercaria in turn developed from *Cercaria flexicauda* Cort & Brooks (1928, pp 183–186) The taxonomy of this species has been discussed in connection with the description of the adult, but the identification and naming really depended upon a knowledge of the life-cycle, which was obtained by means of the following infestation experiments

Metacercaria to adult — Considerations of an *a priori* nature suggested that some of the heavy experimental parasitic infestations of the herring-gulls of Douglas Lake region were obtained from the common suckers of this lake To test this suggestion common suckers, *Catostomus commersonnii* (Lacépède), were fed to two nestling herring-gulls, *Larus argentatus* (Pont), during the summer of 1926 A post-mortem examination of these birds revealed that the intestines of each contained more than one hundred individuals of a species of Diplostomum in all stages of development from metacercariae to sexually mature adults Since both gulls had been obtained from their nesting grounds on June 29, when they were only about one week old, and thereafter had been fed during seven weeks only on cooked fish and the suckers which were given them for experimental purposes, these feeding experiments indicated clearly that the common suckers were the source of the infestation Previous experiments by the Ehrhardt brothers (Braun, 1894, pp 165 167) had demonstrated that *Diplostomum spathaceum* (Rud) developed from a diplostomulum (*Diplostomum volvens* von Nordmann) in Europe It was presumed, therefore, that *Diplostomum flexicaudum* also developed from a diplostomulum La Rue, Butler and Berkhout (1926, pp 285 286) had already pointed out that the crystalline lenses of the eyes of more than 94 per cent of the common suckers of Douglas Lake were heavily infested with metacercariae, which averaged more than thirty in each eye Hughes and Berkhout (1929, pp 483 486), after a careful study of these metacercariae, considered them all to belong to one species of diplostomulum, and my observations led me to accept their interpretation Therefore it was concluded from the experiments of 1926 that the diplostomulum of the eyes of the common sucker of Douglas Lake developed into the adult Diplostomum found in my experimental herring-gulls

This conclusion, drawn from the experiments of 1926, was carefully tested during the summer of 1927 Two herring-gulls about one week old were obtained from their nesting grounds and kept in cages where their food was under complete control, except for insects which might enter the cages The birds were fed cooked fish and occasionally pieces of fresh beef The water supplied to them was pumped from a well In the course of the experiment one hundred and thirty-nine eyes of common suckers were fed to the two gulls between July 9 and August 8 One of the birds was killed on August 8, and the other on August 13 They were carefully examined for their parasites and each was found to contain more than two hundred *Diplostomum flexicaudum* in various stages of development The gull killed first contained some individuals developed only slightly beyond the diplostomulum stage The uniform results of these repeated experiments established beyond doubt that the diplostomulum of the eye of the common sucker of Douglas Lake is the metacercaria of *Diplostomum flexicaudum*

The eggs — On August 8, just before the first gull was killed, several hundred eggs were collected from the feces of both gulls The eggs, carefully separated from all solid matter and repeatedly washed in clean water, were kept in well water in labeled watch glasses The development of miracidia in these eggs was observed from time to time, but was not carefully studied Since all the strigeids, *sensu lato,* found at the autopsy of these gulls belonged to this one species, there is no doubt that these eggs also belonged to the same species

Miracidia - Miracidia were first observed in the dishes containing the eggs on August 27, nineteen days after the eggs were collected, and thereafter they appeared daily for about two weeks They hatched in larger numbers during the morning than during afternoon or night The explanation for this phenomenon may be found in the method of hatching of the miracidium The loosening of the operculum of the egg is probably a chemical, rather than a mechanical, process, depending upon a secretion of the miracidium rather than upon the pressure exerted by the miracidium Barlow (1925, p 24) discussed such an explanation for the hatching of the miracidium of *Fasciolopsis buski* and it seems to me to be a plausible explanation for the hatching of this miracidium The rate of development doubtless varies directly with the temperature and consequently development continues more slowly during the night, but hatching is apparently delayed by darkness, possibly because light stimulates the production of the secretion employed in loosening the operculum These miracidia are positively phototactic toward diffused light In a darkened room they appeared to show some preference for the dimly lighted side of a watch glass They usually swim near the surface of the water In this stratum the snails into which they penetrate are also found in largest numbers during the daytime

A reason for believing that the eggs from which these miracidia developed all belonged to one species has already been stated An additional reason for this belief may now be given, for a detailed study showed that the miracidia were similar in all respects They are described below

Infestation experiments with miracidia upon snails - In eight infestation experiments from August 31 to September 6 the following snails were exposed to these miracidia, or miracidia and eggs *Planorbis trivolvis* Say, *Lymnea stagnalis perampla* Walker, *L lanceata* Gould, *L emarginata angulata* Sowerby, *Physa parkeri* ' Currier ' De Camp, *Physa gyrina* Say and *Planorbis campanulatus* Say These snails, most of them about half-grown, had been collected from Douglas Lake more than three weeks before the infestation experiments began and during that time they had been kept in aquaria in the laboratory Here infestation with miracidia was impossible, for they were kept in well water and were fed lettuce which had been grown far from the lake In each of the eight experiments miracidia were placed in water in watch glasses together with a specimen of several species of the snails named above and they were observed under a dissecting microscope, but in no case was the actual penetration of a miracidium into a snail observed Thereafter the miracidia, together with eggs in some instances, and the snails were kept in labeled bottles where the snails were cared for in the same way as they had been in the aquarium

Miracidia to cercariae — On October 15 and 16 three of the eight experiments involving miracidia of *Diplostomum flexicaudum* and the snails yielded positive results, since one snail of each of these three experiments produced cercariae In one of these experiments the snails had been exposed to three miracidia and twenty embryonated eggs on August 31, and in each of the other two experiments, to twelve miracidia on September 1 It is noteworthy that the weather was unusually warm during the two days when these infestation experiments were performed and that the number of miracidia which hatched was greatest during that time The miracidia also appeared to be extraordinarily active In the three experiments yielding positive results all of the seven species of snails named above were represented, but the cercariae came only from three specimens of *Lymnea emarginata angulata* Sowerby A careful, detailed study of these cercariae showed that they were similar in all respects and consequently that they belonged to one species Professor W W Cort confirmed my identification of them as *Cercaria flexicauda* Cort & Brooks, 1928 Three kinds of evidence warrant the conclusion that *Cercaria flexicauda*, obtained in three of my experiments, resulted from my experimental infestation of the snails with miracidia The water in which the snails exposed to the miracidia were kept was carefully watched for the appearance of cercariae, but none were found in it until forty-five days after the experiments This period agrees with the results of the experiments of Mathias (1925, p 63) upon *Strigea tarda* (Steenstr), in which a corresponding development required six weeks, and also with the result of my experiment (Van Haitsma, 1930) upon *Cotylurus michiganensis* (La Rue), in which the time of development from miracidia to cercariae was forty days The alternative that my snails were already infested with miracidia when they were collected from Douglas Lake would imply that the development of *Cercaria flexicauda* from miracidia during the warmest season of the year required more than sixty days, a conclusion that seems unreasonable The fact that all three of my experiments were consonant in all respects also shows clearly that *Cercaria flexicauda* resulted from my experimental infestation of *Lymnea emarginata angulata* with miracidia Moreover, the later described infestation experiments with *Cercaria flexicauda* on suckers demonstrated that these cercariae continued their development in the crystalline lens Therefore it is concluded that *Cercaria flexicauda* is the larva of the Diplostomum obtained by me from the herring-gull

Snail host of the miracidium — From the fact that I obtained *Cercaria flexicauda* from *Lymnea emarginata angulata* only, it should not be inferred that this species of snail is the only possible host of this cercaria Cort and Brooks (1928, pp 183–186) obtained it from the following snails *Lymnea emarginata angulata* Sowerby, *L stagnalis appressa* Say, *L stagnalis perampla* Walker and *L humilis modicella* Say It is not clear why only one species of Lymnea proved to have become infested with miracidia in my experiments, since other species of this genus of snails were exposed to the miracidia at the same time Several of my exposed snails died during the experiments It may be that some of them died owing to unobserved infestations During my experiments no definite response of the miracidium of *Diplostomum flexicaudum* to the presence of any species of snail was observed For these reasons I do not infer such a definite host specificity for this miracidium as the results of my experiments seem to indicate

Infestation experiments with cercariae upon suckers — In order to complete this life-cycle experimentally three infestation experiments were performed with cercariae of *D flexicaudum* on suckers by pouring small amounts of water containing the cercariae into the aquaria containing the fishes These experiments demonstrated that the cercariae penetrated the fishes and severely irritated them during the penetration In all of my experiments the suckers died too soon after the penetration of the cercariae to permit the metacercariae to develop fully Post-mortem examination of the fishes revealed large numbers of partially developed metacercariae in their eyes, and some within the lens capsule Since the cercariae penetrate all parts of the bodies of the fishes, the experiments demonstrate clearly that the metacercariae normally inhabit the crystalline lens and to this extent present evidence for the genetic connection of the stages of this life-history already mentioned These experiments will be described in greater detail below in connection with the discussion of the cercaria Reasons will also be presented there for the belief that this parasite is the cause of numerous deaths of fishes in nature and in breeding ponds, and that it is therefore of considerable economic significance

THE MIRACIDIUM

Form and measurements — This miracidium is fusiform, widest about one third of its length from the pointed anterior end, and roundly truncate posteriorly Its outline is nearly circular in anterior view A moderately extended specimen measured under a cover-glass is about 0 17 mm long and 0 04 mm wide at the level of the two conspicuous eyespots (Fig 24) The eyespots are normally found in the region of the greatest width The shape and measurements of the miracidium may differ very much in different contraction states In a greatly contracted specimen the length may be one half as great and the width may be almost twice as great as the corresponding measurements of a moderately extended specimen

Movements — The movements of the miracidia of *Diplostomum flexicaudum* are more even and appear to be more purposeful than those of Paramoecium Barlow's (1925, p 27) description of the movements of the miracidia of *Fasciolopsis buski* (Lankester) are applicable here, for the present miracidia also swim about as if they were eagerly seeking something Although these miracidia can back away from solid objects, their movements are usually forward Ordinarily when they are swimming in a watch glass their eyespots remain on the upper side, but occasionally one may be observed to roll about on its long axis without changing its rate of progress At times, a miracidium may cease its forward movement and employing either its anterior or its posterior end as a pivot may spin about so that its movement circumscribes a cone If a miracidium under a cover-glass comes in contact with an air bubble, it may slowly glide along the surface of the bubble while constantly attempting to penetrate the surface film with its protrusile anterior end Similar penetrating movements have also been observed in miracidia which came in contact with a slip of paper employed to hold up the cover-glass The actual movements of penetration of a miracidium of this species into a snail have not been observed

Cilia — These miracidia swim by means of cilia which are about ten micra in length The cilia completely cover the body except at the anterior tip and at the two conspicuous lateral processes found on each side of the body immediately in front of the level of the eyespots and between the epidermal plates On the dorsal surface of the miracidium of *Strigea tarda* Mathias found a rectangular area, free from cilia, directly above the eyespots Such a non-ciliated area was not found in the present miracidium Ciliary movements are maintained unceasingly as long as the animal is alive Even if the anterior part of the body is ruptured so that its cells flow out, the cilia on the posterior part of the organism may still continue to beat for a long time

Eyespots and nervous system — The most conspicuous organs of the miracidium are a pair of dark brown, almost black, eyespots, which are located dorsally and laterally in the region of greatest width They have the form of thick hemispherical bowls and are composed of numerous spherical, melanotic granules From the laterally directed concavity of each eyespot two lenses protrude outward and forward Underneath the eyespots there is a mass of comparatively large spherical cells with granular contents The extent of this mass of cells appeared to vary in different specimens and its outline was difficult to determine, but numerous attempts to determine its shape led to the conclusion that it is bilobed (Fig 24) Cort (1919, pp 511–516) represents the nervous systems of the miracidia of *Schistosoma mansoni* and *Sch japonicum* as oval to quadrangular, and Sewell (1922, p 285) figures the nervous systems of the miracidia of *Sch haematobium* and of Cercaria Indicae XV as circular in outline Mathias (1925, p 37) describes the nervous system of the miracidium of *Strigea tarda* as circular in dorsal view, while Barlow (1925, p 23) represents this organ as irregularly rectangular in the miracidium of *Fasciolopsis buski* These differences in the descriptions of the nervous system are probably in part indicative of the difficulty experienced in determining its outline Nerve filaments proceeding from its cells, such as Barlow (1925, p 23) observed to extend forward and backward from this organ in the miracidium of *Fasciolopsis buski*, were not seen in the miracidium of *D flexicaudum* Faust (1924, p 28, and Fig 11) has described the central neural mass of *Schistosoma japonicum* as circular in outline in dorsal view, but his Figure 11 also shows masses of gland cells at the sides of the neural mass, so that the neural mass and the masses of gland cells together have a more bilobed shape I was not able to distinguish gland cells as described by Faust In fact his observations on this point have not been confirmed by other workers

Primordial digestive organ — Extending along the median region of the anterior part of the body to its tip there is a clavate rudiment of a digestive system which is composed of large cells In some specimens this club-shaped organ seemed to extend ventral and posterior to the brain, but its extent posteriorly could not be definitely determined In the anterior part of the body this organ was more distinctly visible and it appeared to be more rigid than the surrounding tissue This rigidity is doubtless due to the turgidity of its cells In keeping with its appearance of greater rigidity the protoplasm of its cells was more densely granular In the present miracidium there were slight indications of an internal canal in this organ A similar hollow digestive organ was reported for the miracidia described by Sewell, Mathias and Barlow Although this may be a rudimentary digestive organ, as is generally supposed, its position and rigidity suggest that it also performs an important function during the penetration of the miracidium into a snail "Salivary glands," such as Sewell described for the miracidia of *Sch haematobium* and Cercaria Indicae XV, could not be definitely discerned

Excretory system — As in other Strigeata (La Rue, 1926 p 276), there are two pairs of flame cells in the miracidium of *D flexicaudum* (Fig 24) The anterior pair is located near the dorsal surface a short distance behind the eyespots and the posterior pair is found in the lateral posterior region, between the third and fourth quarters of the body The flame cells are large in proportion to the size of the body and their flickering appearance becomes more distinctly visible as the water under the cover-glass is diminished The proto-nephridial systems of the two sides of the body are not connected with each other On each side of the body capillaries extend from the anterior and posterior flame cells to a point about half-way between them, where they unite to form a main collecting tubule From its point of origin each main tubule extends forward almost to the eyespot on the same side of the body Here the main tubule bends posterad and continues almost directly to the region of the posterior flame cell where, after forming a double coil, it arches forward and outward to the excretory pore Each excretory pore opens to the outside laterally near the level of the posterior flame cells Between the organs of the interior and the body wall of the miracidium there is a space in which the main excretory tubules are dilated into little ampulliform bladders just before they open through the excretory pores These bladders are closely similar to those observed in the furcae of the cercariae of this species Since the internal organs are attached to the body wall at only a few points, especially at the anterior and posterior ends of the miracidium, and since these internal organs are independently contractile, there is an almost constant shifting of the relative position of the organs with reference to points on the body wall Thus the posterior flame cells may be found either before or behind the openings of the excretory pores The internal organs may also shift their positions with reference to each other So, for example, the posterior flame cells may point mesad instead of posterad This shifting of the internal organs and the changes in their shape make difficult the accurate detailed description of a typical miracidium

Epidermal plates — The cilia covering the miracidium project from epidermal plates, arranged in four transverse tiers (Fig 20) The plates of the two anterior tiers could readily be distinguished in moribund specimens, but those of the two posterior tiers were more difficult to distinguish These plates, as seen in optical section, appear to have thick bands somewhat resembling cell walls extending from their external to their internal surfaces (Figs 21–23) The studies of Thomas (1883), Schubman (1905) and Ortmann (1908) upon the embryological origin of the plates and of Coe (1896) on their structure have shown that each plate represents a single cell Nuclei were not seen In moribund specimens the ectodermal plates were sometimes sloughed off severally, each as a unit Only in this way was their number in the two posterior tiers determined In a dorsal view the foremost tier showed three plates, the second four, the third two, and the fourth one and one half If one assumes that the dorsal and ventral surfaces are alike with respect to the number of plates, there are twenty-one plates in all, the same number which Mathias (1925, p 38) found in the miracidium of *Strigea tarda* The boundary between the first and second tiers of plates is found immediately in front of the eyes, that between the second and third tiers is located near the middle of the body, and that between the third and fourth tiers crosses the miracidium immediately behind the excretory pores

Lateral processes — Lateral processes similar to the larger lateral processes of this miracidium (Figs 20–24) have been represented for the miracidia of *Sch mansoni* and *Sch japonicum* by Cort (1919, pp 511–516) and of *Sch haematobium* and Cercaria Indicae XV by Sewell (1922, p 285), but both these investigators represent only one process on each side of their respective miracidia Cort called these processes anterior ducts Sewell (1922, p 287) believed that the similar processes of the miracidia of Cercaria Indicae XV and *Sch haematobium* are connected with excretory canals which he supposed to lie between the ectodermal plates of the first two tiers

In the miracidium of *D flexicaudum* there are two lateral processes in series on each side and situated at the level of the boundary between the two anterior tiers of plates The posterior process is always the larger The cuticle of this lateral process is thin and is bulged outward According to Faust (1924, p 28), similar processes in the miracidium of *Sch japonicum* represent the ends of ducts carrying to the outside a mucoid secretion from glands lying at the sides of the central nerve cell mass, but such an explanation for the larger lateral processes of the present miracidium was not indicated by my observations The smaller anterior process on either side appears to be a thin outwardly bulged portion of the cuticle of an epidermal plate

Inasmuch as lateral processes have been observed in the miracidia of three genera of the Strigeidae, viz , Diplostomum, Cotylurus and Crassiphiala, as well as in the miracidia mentioned above and described by Cort, Sewell and Faust, it is remarkable that Mathias (1925, p 37) did not find such processes in the miracidium of *Strigea tarda* Mathias showed a projecting ring of tissue encircling his miracidium immediately in front of the eyespots Such a ring was not observed in my miracidia Possibly Mathias misinterpreted these processes as optical sections of a ring The lateral processes of the miracidium of *D flexicaudum* are found only at the sides of the body, as was evident from an anterior view and also from the appearance of the rotating miracidium

Primordial germ cells — In the posterior end of the miracidium of *D flexicaudum* a variable number of large granular cells are arranged in a longer or shorter row which forks anteriorly Corresponding cells in the miracidium of *Sch mansoni* as described by Cort (1919, pp 511–516), and of *Sch haematobium* and of Cercaria Indicae XV described by Sewell (1922, pp 285–287), have been interpreted to be primordial germ cells The foremost of these cells may be separate from the rest, become rounded and lie free in the miracidium Mathias did not describe similar cells in the miracidium of *Strigea tarda* The interpretation of these cells is of considerable interest, for it involves the explanation of the method of formation of the daughter sporocysts Investigators are agreed that miracidia upon penetration into their proper snail hosts develop into mother sporocysts, but opinion is divided concerning the method of formation of the daughter sporocysts (Sinitzin, 1909, pp 664–682, Mathias, 1925, p 45)

THE SPOROCYST

Description and contents — On December 17, 1927, a snail which had been producing cercariae for more than two months was examined for its sporocysts Upon removal of the shell of the snail it was observed that its digestive gland had a mottled appearance due to the fact that it was riddled with sporocysts The color of the sporocysts is pale yellow, lighter than the color of the digestive gland which is brown The sporocysts are long, unbranched, thread-like tubes (Fig 26) In living material their walls appear thin and granular They are so delicate that they could not be separated from the digestive gland of the snail without breaking The largest pieces which were freed from the snail were almost 1 mm long Each piece was constricted more or less at irregular intervals and bore some resemblance to a string of sausages On account of the constrictions the diameter of a sporocyst may be twice as great in one place as in another A large sporocyst measured about 0 1 mm in diameter in the internode between the constrictions From unbroken ends of pieces of sporocysts it could be determined that one end of a sporocyst is closed and rounded, and that the opposite end contains a narrow birth-pore (Fig 25), so narrow that the cercariae must enlarge its opening considerably in order to escape through it Figure 25 shows that the birth-pore is not exactly in the center of the end of the sporocyst In cross-sections it appeared that the wall of the sporocyst was thin in some places where it consisted of only one subcuticular layer, and in other places thicker where the cuticle was lined with several layers of cells Within the sporocysts were found large spherical cells with conspicuous nuclei, cell masses varying in shape from spherical to ovoid, and fully developed cercariae (Fig 26) In other parts of the sporocyst a fibrous network with small scattered nuclei was observed The large cells were probably ova, the cell masses represent germ balls developing into cercariae

THE CERCARIAL STAGE

Identification — Cercariae of this species were obtained October 15 and 16, 1927, from three specimens of *Lymnea emarginata angulata* Sowerby, from which they escaped into the water They were carefully studied and tentatively identified as *Cercaria flexicauda* Cort & Brooks, 1928 My description, together with some specimens fixed and preserved in hot 5 per cent formalin and others stained and mounted on slides, was sent to Professor W W Cort, who confirmed my identification For a description of this cercaria the reader is referred to the work of Cort and Brooks (1928, pp 183–186)

Infestation experiments — Two hog-nosed suckers, *Hypentelium nigricans* Le Sueur, which had been caught in the Huron River near Ann Arbor and kept in an aquarium in the laboratory for five weeks, were exposed to these cercariae on October 19 That the cercariae penetrated them was evident from the actions of these normally sluggish fishes They became exceedingly active and swam about in the aquarium in a spasmodic erratic fashion Sometimes they also made quick oscillating movements from side to side as if to brush away a source of irritation At other times they frantically leaped from the water Four days after the exposure to the cercariae it was discovered that they were severely infested with a protozoan parasite, Ichthyophthirius Treatment to kill the Ichthyophthirius also killed the fishes Thereupon the eyes of one of the fish were examined and more than one hundred developing metacercariae were found in them. That these were the same species of cercariae to which the fish had been exposed was clearly shown by the seven rows of spines on the spiny cap at the anterior end. No well-developed specimens of diplostomulum were found. The presence of these young metacercariae in the eyes demonstrates conclusively that this cercaria is a form which normally lives in the eye.

Another hog-nosed sucker, about 5 inches long, which had been kept in the laboratory for one week, was infested with the same species of cercariae on November 3, 7 and 10, 1927. The fish reacted to the penetrating cercariae as the two previously described hog-nosed suckers had done. At times it leaped entirely out of the water, just as fishes have often been observed to do in lakes. Probably the similar movements of fishes in lakes are also due in part to the penetration of cercariae. The eyes of this fish appeared bloodshot on November 7 with a wide blood-colored ring around each pupil. Between this red ring and the pupil there was a narrower pale yellow ring. A red streak probably due to congestion of blood was also noted at the base of each pectoral fin. These symptoms remained until November 11 when the fish was found dead at the bottom of the aquarium. At that time the eyes, which noticeably protruded from the head, were removed for examination. Under a lens parasites could be seen through the black pupil as whitish flakes. Attempts to tear open the eyeballs revealed that they were unusually turgid and hard, a condition resembling glaucoma. The choroid coat of the eye was congested with blood. About one hundred cercariae were collected from the eyes and fixed in corrosive-acetic at about 80° C for future study. No fully developed metacercariae were found. The metacercariae appeared to be in about the same stage of development as in the two previously described hog-nosed suckers, but some of them had already entered the crystalline lens.

A common sucker, *Catostomus commersonnii* (Lacépède), about four inches long, which had been kept in the laboratory about one month, was exposed to the cercariae of *D. flexicaudum* on December 14. The responses of the common sucker to the penetration of these cercariae were similar to those of the hog-nosed suckers described above On the following day, however, this fish was found dead on the bottom of the aquarium

Pathological effects upon fishes — There is no doubt that the penetration of large numbers of the cercariae of *D flexicaudum* (Cort & Brooks) into both species of suckers of the two experiments last described was the cause of the death of these fishes The results of my experiments agree with the experience of Blochmann (1910, pp 47–49), who accidentally placed eight specimens of *Lymnea stagnalis* in an aquarium with several fishes The next morning all the fishes in his aquarium were dead Examination showed that furcocercous cercariae, *Cercaria fissicauda* La Val, were escaping from the snails In order to determine whether these cercariae caused the death of his fishes he performed several infestation experiments with *Cercaria fissicauda* on fishes of different genera and also on salamander larvae In every experiment the result of the experimental infestation was the death of the vertebrate By careful experiments he eliminated other possible explanations than cercarial infestation for the death of his fishes He also performed an experiment which indicated that the death of his fishes was not due to toxins produced by the cercariae and therefore he supposed that mechanical injuries inflicted by cercariae upon their hosts were the causes of death Blochmann examined the blood and brain of an experimentally infested fish and found cercariae in them as well as in other tissues From his observations he concluded that the movements of the cercariae through the tissues, particularly of the vascular and nervous systems, were the most probable causes of the death of his fishes

The reactions of Blochmann's fishes to the penetration of cercariae were similar to those which I have observed in my experimental fishes, but mine did not die so quickly, probably because my cercarial infestations were not so heavy Owing to the fact that Blochmann's fishes died very quickly he did not observe such marked symptoms of infestation as I did

Economic significance — These experiments indicate that fishes in breeding ponds and in nature which swim into areas inhabited by snails producing strigeid cercariae may be killed by the penetration of large numbers of these cercariae It is believed that of the thousands of fishes which are at times washed up on our lake shores every summer the deaths of a considerable percentage are due to mass infestations of furcocercous cercariae Szidat (1927, pp 83–90), who made definite observations on the causes of the death of fishes in the Kurischen Haff in connection with his life-history study of *Diplostomum spathaceum* (Rud), concluded that the cercariae of this species in European lakes caused the death of thousands of *Acerina cernua* and *Leuciscus rutilus* Although I have not made a careful study of the causes of the death of fishes at Douglas Lake, my observations on fishes in nature support the belief that large numbers are killed by strigeid cercariae in this country also I have seen epidemic deaths of fishes under conditions similar to those observed by Szidat Some of these fishes showed bloody spots and streaks and abnormally congested bulging eyes, just as Szidat described Consequently, I too conclude that the cercariae of *D flexicaudum* cause the death of a large proportion of the thousands of fishes which are found on the shores of Douglas Lake every summer Since this species is the most numerous of all kinds of furcocercous cercariae found in Douglas Lake (Cort and Brooks, 1928, p 183), it probably is also a proportionally important cause of the death of fishes there

My experiments, those of Blochmann (1910, pp 47–49), and of Cort and Brown[1] have shown that strigeid cercariae will penetrate and may kill other fishes than those in which they normally develop Consequently, the deaths not only of the common suckers of Douglas Lake, but also of other fishes may be due to the cercariae of *D flexicaudum* Likewise, the deaths of the common suckers of Douglas Lake are doubtless due not to this species of cercaria alone, but also to other strigeid cercariae On this account it appears that these fatal epidemics among fishes cannot be prevented by the destruction of a few species of snails, since many kinds of snails and cercariae are involved in the deaths Though a reduction of the number of Lymneidae in a lake, as Szidat (1927, pp 83 90) proposed, will help to reduce the mortality rate of fishes, it is hoped that a careful study of the physiological requirements of miracidia and cercariae will suggest more practicable measures for the conservation of our fishes

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[1] Professor W W Cort and Dr H W Brown have kindly permitted me to publish their records of the results of infestation experiments with cercariae of *D flexicaudum* upon three kinds of fishes and also upon frog tadpoles The fishes employed in these experiments were obtained from Vincent Lake, an acid lake (Jewell and Brown, 1924 pp 77–84) in which the fishes were known to be free from trematode infestations. Fourteen yellow perch *Perca flavescens*, and about one hundred young bull heads, *Ameiurus nebulosus* were exposed to these cercariae About one month later the fishes of both species which still survived contained variable numbers of not yet fully developed metacercariae in the lenses of their eyes A similar exposure of two small pickerel, *Esox lucius*, yielded, six weeks later, fully developed specimens of diplostomulum in their crystalline lenses Other experiments proved that these cercariae readily penetrated other kinds of fishes Tadpoles exposed similarly contained only degenerating cercariae, also in their eyes after one month

As already explained in the introductory description of the life-history of this species, there are often found in nature common suckers which have large numbers of fully developed diplostomula of *D flexicaudum* in the lenses of their eyes Usually these fishes do not show marked symptoms which can be attributed to their infestations The infestation has doubtless taken place so gradually that the injuries inflicted by the penetrating cercariae were not fatal Fatal injuries are inflicted only when large numbers of cercariae penetrate the fishes at the same time After the metacercariae have lodged in the crystalline lenses of the eyes they probably are not severely injurious unless they are present in large numbers (Hughes and Berkhout, 1929, p 484) Thus it can be explained that the common suckers of Douglas Lake may harbor thirty metacercariae of *D flexicaudum* in the lens of each eye without succumbing to the infestation

THE DIPLOSTOMULUM

Host and habitat — As explained in the introductory description of my feeding experiments, an average of thirty diplostomula of *D flexicaudum* was found in 94 per cent of the common suckers of Douglas Lake by La Rue, Butler and Berkhout (1926, pp 284–286) They were found in the lenses and not in the humors of the eyes These metacercariae are not encysted and they appear to be all of one kind Their morphology has been described by Hughes and Berkhout (1929, pp 483–488) and therefore is not discussed here In this connection it is significant to note that the metacercariae of *Diplostomum spathaceum* (Rud), called *Diplostomum volvens* von Nordmann by Braun (1894, pp 165–167) in the description of the feeding experiments performed by the Ehrhardt brothers and also by Szidat (1927, pp 83 90) in the description of the life-history of this species, was found in both the lenses and the humors of the eyes of *Acerina cernua* and *Leuciscus rutilis* But the fully developed diplostomula of *D flexicauda* were found only in the lenses of the eyes of the common suckers, *Catostomus commersonnii*, the only species of fishes in which I have studied them Because of the morphological differences described by Hughes and Berkhout (1929, pp 483–488), it appears justifiable to **distinguish** specifically between the diplostomulum of *D spathaceum* and that of *D flexicaudum* The belief that they are distinct species is also strengthened by my comparative study of the adults, presented in Part I of this paper

Summary of life-history - The rate of development of *D flexicaudum* doubtless varies with the temperature, but at summer temperatures in Michigan development proceeds approximately as indicated in the following outline

Eggs in the feces of the herring-gull are deposited in water From these eggs miracidia hatch in about three weeks After escaping from the eggs the miracidia penetrate *Lymnea emarginata angulata* Sowerby, and probably other snails, within a few hours Inside the snails the miracidia transform into mother sporocysts which in turn produce daughter sporocysts Within the latter cercariae develop in about six weeks after the penetration of the miracidium into the snail The cercariae escape from the snails and lead a free-swimming life for less than a day They penetrate various parts of the body of the common sucker and travel to the eyes of these fishes, finally coming to rest within the lens capsule, where they grow and metamorphose into the diplostomulum stage It probably takes about five or six weeks from the time that the cercariae penetrate into the fishes before the diplostomulum has reached the infective stage When common suckers are eaten by herring-gulls the diplostomulum attains sexual maturity in their intestines in less than one week The length of life of the adult *D flexicaudum* within the gull was not determined

The life-cycle of *D flexicaudum* agrees in general with the description of the life-cycle of *D spathaceum* as described by Szidat (1927, pp 85–86), but Szidat does not explain the time required for the development of each stage The snail and fish hosts of the two species differ The rate of development of *D flexicaudum* appears to agree quite closely, according to results in this paper (also Van Haitsma, 1931), with that of *Cotylurus flabelliformis* (Faust) and *C michiganensis* (La Rue) (Van Haitsma, 1930), and also with that of *Strigea tarda* described by Mathias (1925)

The miracidium and the sporocyst have been carefully described, the former in considerable detail The cercaria has been described by Cort and Brooks (1928, pp 183–186) and the diplostomulum by Hughes and Berkhout (1929, pp 483–486) Description of the adults and a comparison of adults with related forms has been made in Part I of this paper

The economic importance of the cercaria is considered Studies of the results of infestation experiments of the cercariae in fishes are discussed They indicate clearly that the penetration of large numbers of these cercariae into fishes causes the death of the fishes The conclusion is drawn that the cercariae of *D flexicaudum* also cause the death of large numbers of fishes in breeding ponds and in nature

ACKNOWLEDGMENTS

This study was conducted under the direction of Professor George R La Rue, whose helpful suggestions have been invaluable Professor W W Cort confirmed the identification of the cercaria The fishes and snails employed in the experiments were identified by Dr Carl Hubbs and Miss Mina L Winslow, respectively For all of this help,'generously given, I wish to express my cordial gratitude

CALVIN COLLEGE
GRAND RAPIDS, MICHIGAN

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EXPLANATION OF PLATES

The reference lines near the figures represent 0.1 mm.

ABBREVIATIONS

ac — acetabulum
ag — adhesive gland
bp — birth pore
ct — collecting tubule
cut — cuticle
cvd — common vitelline duct
dc — digestive cecum
dej — ductus ejaculatorius
dex — dorsal excretory vessel
ds — digestive organ
egc — egg cell
ep — epidermal plate
epl — epidermal layer
ex — excretory vessel
exp — excretory pore
ga — genital atrium
gb — germ ball
gc — germ cell
l — lens
lc — Laurer's canal
lp — lateral process
lsc — lateral sucking cup
mg — Mehlis' gland
mvex — median ventral excretory vessel
n — nerve strand
ns — nervous system
oot — oötype
ov — ovary
ovd — oviduct
rvd — right vitelline duct
t_1 — anterior testis
t_2 — posterior testis
ut — uterus
uta — uterus ascendens
utd — uterus descendens
vd — vas deferens
ve_1 — vas efferens of t_1
ve_2 — vas efferens of t_2
ves — vesicle
vex — ventral excretory vessel
vit — vitelline follicle
vr — vitelline reservoir
vs — vesicula seminalis

EXPLANATION OF PLATES XLIII–XLV

PLATE XLIII

Fig. 1. Reconstruction showing external form, distribution of vitellaria and digestive system of *D. flexicaudum*. Right side view.

Fig. 2. Reconstruction of male reproductive system of *D. flexicaudum*. Right side view.

Fig. 3. Reconstruction of cross-sections, showing the coils of the seminal vesicle of *D. flexicaudum*.

Fig. 4. Reconstruction of cross-sections of *D. flexicaudum*, showing the relation of the ejaculatory duct and the uterus to the genital atrium.

Fig. 5. Reconstruction of cross-sections of *D. flexicaudum* showing the relation of the vasa efferentia to the vas deferens and anterior testis.

Fig. 6. Reconstruction of cross-sections showing the relation of the vitelline reservoir, common vitelline duct, oötype, Mehlis' gland and ascending uterus. Anterior view.

FIG. 7 Reconstruction showing the relation of the ascending uterus to the ovary oviduct, and Laurer's canal Anterior view

FIG 8 Right side view of the ovary and the junction of Laurer's canal with the oviduct

FIG 9 Right side view of the intertesticular coils of the uterus

FIG 10 Right side view of the female genital system

PLATE XLIV

FIGS. 11-19 A series of cross-sections of an early adult developmental stage to show the excretory system

FIG 11 Cross-section of the forebody anterior to the acetabulum

FIG 12 Cross-section of the forebody in the region of the holdfast organ

FIG 13. Cross-section of the posterior end of the forebody

FIG 14 Cross-section of the hindbody at the level of the anterior bend in the uterus

FIG 15 Cross-section of the hindbody through Laurer's canal

FIG 16. Cross-section of the hindbody through the anterior testis

FIG 17 Cross-section of the hindbody through the posterior testis

FIG 18. Cross-section of the hindbody through the bursa copulatrix

FIG 19 Cross-section of the hindbody through the excretory pore

PLATE XLV

FIG. 20 Epidermal plates of the miracidium of *D flexicaudum*

FIG 21 Optical view of epidermal plates and lateral processes of the miracidium of *D flexicaudum*

FIG 22 Relation of larger lateral process to vesicle in the miracidium of *D flexicaudum*. A slightly deeper focus than shown in Figure 21

FIG 23 Optical view of excretory pore of the miracidium of *D flexicaudum*

FIG. 24 A reconstruction of many sketches of the internal organs of the miracidium of *D flexicaudum*

FIG 25 A longitudinal section of the anterior end of the sporocyst of *D flexicaudum*, showing the birth-pore

FIG. 26 An external view of the posterior end of the sporocyst of *D flexicaudum* showing egg cells and germ balls

PLATE XLIII

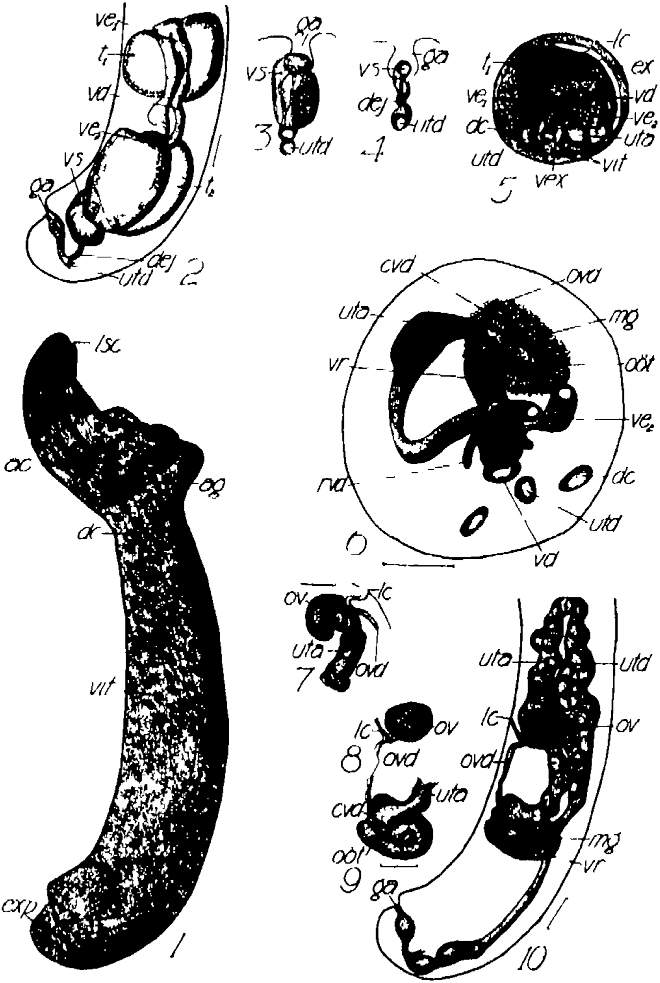
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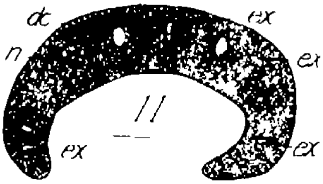
PLATE XLIV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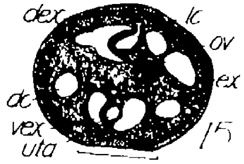
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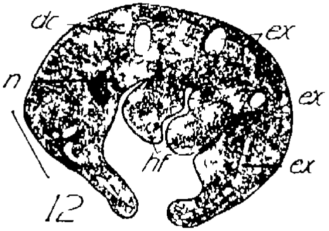
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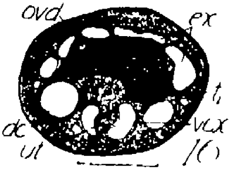
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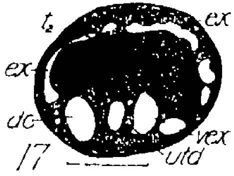
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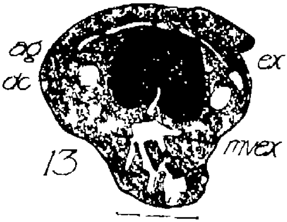
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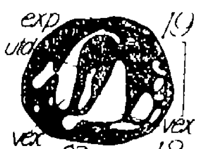
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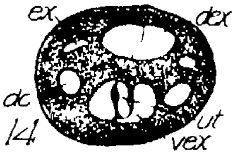
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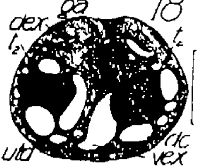
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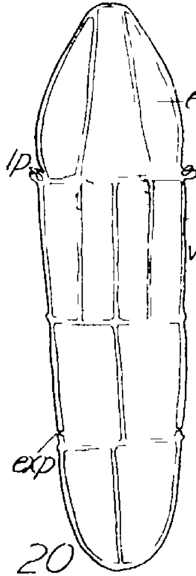
PLATE XIV



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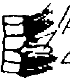

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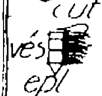

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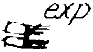

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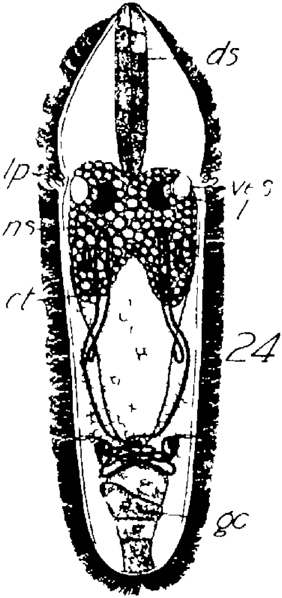

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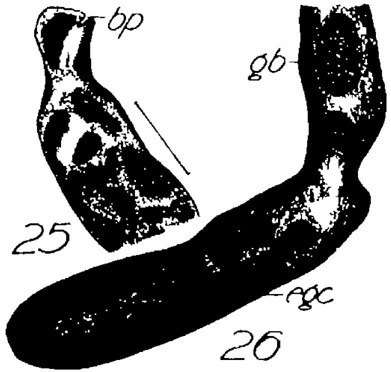

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OBSERVATIONS ON THE LIFE-HISTORY AND CONTROL OF THE FERN SCALE, *HEMICHIONASPIS ASPIDISTRAE* SIGN

W H REGINALD WERNER

I INTRODUCTION

THE fern scale, *Hemichionaspis aspidistrae* Sign , has proved to be of considerable economic importance to the grower of ferns, owing to its rather rapid spread and to the damaging effect it has on the appearance and health of the ferns The investigation included herein was begun in the fall of 1928 and had as its objective the discovery of the essential details of the life-history of this coccid and the development of methods of control This study extended over a period of about six months and was carried out at the University of Western Ontario, London, Ontario

This problem was suggested by Professor J J Davis of Purdue University, Indiana, and was directed by Dr J D Detwiler of the University of Western Ontario, to whom grateful acknowledgment is due for his valued advice and interest I am indebted also to Professor J W Burns, department of chemistry, University of Western Ontario, for advice in connection with the formulation of sprays, to Messrs Harold Morrison and A B Gahan, United States Department of Agriculture, Washington, D C , for taxonomic aid; to Mr H F Dietz, assistant state entomologist of Indiana, and Professor G F Ferris, Stanford University, California, for advice regarding systematic history, and to the various greenhouse proprietors of the city of London, who so kindly allowed me the freedom of their greenhouses In conclusion, I wish to acknowledge gratefully the assistance of Professor Paul S Welch, University of Michigan, in the preparation of this manuscript for publication

II GENERAL DISCUSSION

Hemichionaspis aspidistrae is sometimes known as the "fern scale," or as the "stationary white fly" The latter name is due to the general resemblance in appearance of the male scales to *Trialeurodes vaporariorum* West , the greenhouse white fly

Information received from Messrs Harold Morrison and H F Dietz and Professor G F Ferris leads the author to believe that many coccid workers are now placing this species in the genus *Pinnaspis*

Injury and dispersal

This scale, though not, as a rule, a serious pest in most greenhouses, often becomes quite numerous on the ferns kept in houses, offices and small ferneries Some greenhouses, however, become badly infested with it and the owners usually find it hard to eradicate

The injury caused to the ferns by this scale is peculiar in that it, especially the male form, causes a distinct, small, yellowish-white blotch on the leaflet This soon makes the frond unsightly, and, if the infestation is heavy enough, ultimately causes the death of the frond

Once established in a greenhouse, the scale spreads rapidly, if one considers that its chief means of transportation is by crawling from one fern to the next one in contact with it Of course, it is greatly aided by transference of the infested ferns from place to place in the greenhouse or by any jarring of fronds overhanging a neighboring fern One greenhouse was visited on November 1, 1928, and a large number of the ferns examined for this scale, but no scale of this species was found It was visited again about the last of December, and, though no thorough inspection was made, there were no scales noticeable However, when the greenhouse was visited on February 23, 1929, practically every large potted Boston fern was infested to a moderate degree and a great many of the unpotted, young ferns on the benches were also slightly infested A badly infested fern had been sent in to be cleaned up and was probably the source of the trouble

Distribution and host plants

The fern scale is essentially a tropical insect, being found in the colder climate, only in greenhouses. The following are some of the localities listed: Belgium, Brazil, California, eastern Canada, Ceylon, Cuba, England, Formosa, France, Holland, India, Japan, South Australia, Trinidad, eastern United States and West Indies.

H. aspidistrae has a considerable number and variety of host plants, of which a few are: Acacia, Alocasia, Amomum, Areca, Aspidistra, Capparis, Catechu, Citrus, Cocos, Croton, Cyanotus, Ficus, Gaultheria, Helichonia, Orchis, Pothos, Strobilanthus and Thea.

Aspidistra and the Boston fern, *Nephrolepis exaltata* var. *bostoniensis* Davenport, appear to suffer the greatest among the greenhouse plants.

III. DESCRIPTION OF THE STAGES

The egg is ellipsoidal when laid but, as more and more eggs are deposited under the scale, it becomes compressed and misshapen. The color depends slightly on the age of the egg. When newly laid, it is pale brown[1] spotted with light brown ocher blotches; later, however, it becomes almost uniform in color and somewhat lighter than brown ocher. The results of twenty-four egg measurements are given in Table I.

TABLE I

Egg Measurements

	Maximum	Minimum	Average
Length of egg	0.216 mm	0.174 mm	0.196 mm
Width of egg	0.096 mm	0.084 mm	0.091 mm

---

[1] The terminology used for descriptions of color in this paper is derived from the nomenclature of Windsor and Newton's water colors as given in the *Glossary of Entomology* by J. B. Smith.

First instar

First-stage larvae (Pl XLVI, Fig 1) vary in color from pale cadmium yellow to a shade lighter than brown ocher, growing darker with age The eyes, however, are jet black and quite conspicuous Two setae project from the caudal end and are about one half the length of the larval body The antennae are 6-segmented The writer was not able to make out, with any degree of certainty, more than two digitules on the legs of the specimen illustrated in Plate XLVI, Figure 1

On becoming established on a fern leaf the first-stage larva turns much paler It secretes a white, waxy substance between the caudal border and the leaf This is hardly large enough to be called a scale and yet it resembles a scale in its formation

The larvae vary from 0 216 mm to 0 341 mm in length and from 0 108 mm to 0 220 mm in width (Table III) The variation is largely due to the age of the larvae During this part of the life-history the sexes cannot be determined

Second instar

Female - This stage differs quite radically from the first instar The antennae and legs have disappeared and the eyes have become smaller and less conspicuous The thorax has become closely united with the head and the segments are less visible The larva resembles the adult female (Pl XLVII, Fig 4) to a large extent, but is much smaller The general color remains about the same, however Measurements were taken from the second-stage exuviae, since the insect itself can vary greatly by extension and contraction of the body The measurements for width proved too variable to be of value, owing to difference in the amount of curvature of the scale The average length is 0 578 mm , the maximum and minimum lengths are 0 682 mm and 0 528 mm , twenty-four measurements were taken

Scale of female — The scale of the second-instar female resembles the scale of the adult in texture, but is not nearly so extensive, being in length only about one eighth that of the latter

Male (Pl XLVI, Fig 2) — The second-instar male resembles the second-stage female very closely except that it is slightly more elongate and does not grow so large It is about 0 440 mm long

Scale of male — The scale of the male is distinctive and differs greatly from the female scale Dietz and Morrison (1916) describe it as follows "Length about 1-1 2 mm , elongate, slender, sides nearly parallel, distinct and prominently tricarinate, white, exuvia pale yellow, about one-fifth to one-fourth the total length of the scale "

Third instar

Female — As is usual in the Diaspidinae, there are only two female larval instars whereas the male has three

Male — In this stage the male has become more elongate, the rostrum and rostralis are missing, and the antennae, legs, wings and stylus are all partially developed and quite visible, each being inclosed in a cuticular sac This change is carried out under the scale formed in the second instar

Adult

Female (Pl XLVII, Fig 4) — Cooley (1899) gives the following description "The first four segments anterior to the pygidium very pronounced, being often produced at each side into a conspicuous protuberance First and second pairs of lobes well developed, third pair very rudimentary or wanting Each median lobe with three distinct notches on the outer curved edge Lobules of the second lobe long and narrow, spatulate in form edges thickened at the base The gland-spines are arranged as follows 1, 1, 1, 1, 2-5 As a rule the fifth group contains 2 3 spines but in one specimen I observed 5 The marginal gland-orifice between the first and second lobes is situated on a large conspicuous prominence Second row of dorsal gland-orifices wholly absent Third and fourth rows with 2-5 orifices in their posterior groups Anterior groups absent Median group of circumgenital gland-orifices 5-15, anterior laterals, 15-22, posterior laterals, 17 23" (cf Pl XLVII, Fig 3, for pygidium)

Scale of Female (Pl XLVII, Fig 1) — Cooley (1899) also describes the scale as follows ' Length, 1 8 2 6 mm Distinctly broadened posteriorly and usually broadly rounded at the extremity, but occasionally bluntly pointed Very thin and delicate in texture or moderately thick and strong Pale yellowish-brown to brown Exuviae 7 9 mm long, of the same color as the secreted portion of the scale but slightly brighter "

Male (Pl XLVI, Fig 4) – The male is dark in color (described as more or less rosy by Comstock, 1916) The mesothorax is quite long and thus separates the first and second pairs of legs considerably The antennae bear many bristles and consist probably of 10 segments These are rather hard to differentiate The stylus and wings are long and conspicuous Measurements of 10 specimens are given in Table II The measurements of length and of the length of stylus were made to the base of the little swelling on the stylus, as shown in Plate XLVI, Figure 4

TABLE II

MEASUREMENTS OF ADULT MALE

	Maximum	Minimum	Average
Length	0 374 mm	0 264 mm	0 297 mm
Width	0 154 mm	0 132 mm	0 145 mm
Length of stylus	0 209 mm	0 154 mm	0 181 mm

One male was unusually long, 0 473 mm , whereas the measurements of width and length of stylus were normal This probably was a distortion due to pressure of the cover-glass Consequently, this measurement has been omitted from the data

IV LIFE-HISTORY AND HABITS

Egg stage

Incubation period — The incubation period of the scale is rather hard to determine, but some data were obtained by various means On December 28, 1928, while the writer was collecting eggs from under the scales, one was found that evidently had just been laid In fact, it was not completely disengaged from the vulva of the adult This egg was placed on a wax plate and incubated at from 75° to 80° F (cf "Technique," p 536) The relative humidity was approximately 100 per cent since some condensation took place This egg hatched on January 9, 1929, after an incubation period of 12 days

On December 28, 1928, the writer also found an adult that had already laid 3 eggs and another whose eggs were mature in her body The eggs were dissected out of the follicles and oviducts of these insects, placed on wax plates and incubated under the conditions mentioned above The eggs of the latter were attacked by mould and did not mature, but some of the former did Six of these hatched, 2 on January 10 (incubation 13 days), 3 on January 11 (14 days) and 1 on January 12 (15 days)

Some observations were carried out on eggs laid under a scale, this was done by directing a light through the scale (cf "Technique," p 539) One specimen proved to be transparent and especially favorable for study Six eggs were laid by it on February 4, 2 more on February 5 and 1 on February 6 This scale was watched daily and the first hatching took place on February 22, when 4 larvae emerged from under the scale Another one hatched on February 24 The incubation period was, therefore, 18 days, the fern being kept under laboratory conditions, i e relative humidity 60–70 per cent and temperature 70°–85° F

Emergence from egg — When emerging from the egg, the larva bursts the chorion at the anterior end along the sagittal axis This split extends well back behind the eyes, and then the two sides begin to spread apart, forming a V-shaped opening The chorion is gradually spread wider and wider until the opening is as wide as the body The larva then crawls out of the chorion Empty chorions look like little scraps of white tissue paper

Percentage hatching — No actual data were obtained, but it was estimated that of about 2000 eggs handled not over 200 failed to hatch

First stadium

Time before settling down — The length of the active period of larvae varies from half an hour to 24 hours and, under adverse conditions such as having no plant leaves to settle on, they may crawl for 48 hours or more During this time they are usually quite active and may move a considerable distance Some apparently settle down temporarily, and later move to some other place Usually, however, they remain active until they have chosen a spot on which to settle permanently During the crawling period the young larvae are rather easily jarred off the fern and great care has to be taken while one is transferring them to plants Of 535 young scales whose transfer to ferns was recorded, 207 (38 6 per cent) were never recovered Probably these dropped or were jarred off the plants

Two experiments were performed to account for this loss A fern was laid on its side on a table over a piece of clean, white cardboard ruled in squares A binocular was set up over a frond with the stage reversed so as not to move the fern when removing the binocular Transference of 30 larvae was accomplished very carefully and without jarring the fern A ring of bird-lime was laid down on the paper surrounding the area under the infested frond The fern was left for 6 hours in this position before being moved to the incubator for the night When this was done the cardboard was held firmly beneath the frond by means of a rubber band around the flower pot The next day the paper and frond were carefully examined and it was found that 18 larvae had fallen on the paper, 7 were established on the plant and 5 were unaccounted for The temperature varied between 67° F and 79° F

The next experiment was carried out in the greenhouse It was a repetition of the one mentioned above except that the stem of the plant was also ringed with bird-lime and the plant was left absolutely undisturbed for 2 days In this case 29 larvae were transferred to the plant After 2 days it was examined carefully One larva was found established on it, 4 were dead owing to rough handling in the transference, 20 had dropped to the paper, and 4 could not be found

In each case the ferns were sheltered from any strong draft Probably the dropping off of the larvae is a factor in their dispersal to other fronds and other plants

These nymphs show a marked preference for the lower side of the frond as a place on which to settle Out of a total of 229 individuals recorded, 160 (69.9 per cent) settled on the under side of the frond, 36 (15.7 per cent) on the upper side and 33 (14.4 per cent) on the stem.

Formation of scale. — One to two days after the settling down of the larva, fine waxy filaments begin to appear from under the insect and extend into the air above it. From 1½ to 5 days after settling down, the larva takes on a hard chitinous covering which contrasts strongly with the soft covering of the newly hatched insect. During the interval between emergence from the egg and the appearance of chitin, the young first-stage larva increases considerably in size, as shown in Table III. Though having very little supporting evidence, I believe that this interval is prolonged by a high humidity. This point might prove of interest on a spray program, but would have to be more thoroughly investigated. The greenhouse and the incubator in which the plants were kept while in the laboratory were maintained at about the same temperature (about 70° F.), but the greenhouse undoubtedly had a

TABLE III

EXTREME AND AVERAGE MEASUREMENTS OF FIRST-INSTAR LARVAE

	No. of larvae examined	Maximum	Minimum	Average
1. Newly hatched larvae				
Length	24	0.252 mm	0.216 mm	0.234 mm
Width	24	0.126 mm	0.108 mm	0.120 mm
2. Before chitinization				
Length	9	0.324 mm	0.216 mm	0.266 mm
Width	9	0.180 mm	0.110 mm	0.146 mm
3. After chitinization				
Length	10	0.341 mm	0.280 mm	0.311 mm
Width	10	0.220 mm	0.165 mm	0.196 mm
4. First-instar exuviae				
Length	25	0.330 mm	0.264 mm	0.314 mm
Width	7	0.187 mm	0.154 mm	0.174 mm *

* The decrease in width of the exuviae as compared with the width measurements after chitinization is probably due to curvature of the cast skin.

higher humidity These facts were not recorded definitely since I expected to have time later to run special experiments on this part of the problem Consequently, the first experiments were devoted mainly to getting an outline of the life-history The first 7 plants successfully infested (i e Nos 4 11) were kept in the greenhouse for the greater part of the first stadium The remainder were not taken from the laboratory to the greenhouse until after chitinization and scale formation had been observed Thus plants 4-11 were in the greenhouse for all but one day during the period previous to chitinization, but the other plants recorded were not in the greenhouse at any time during this period A marked difference is noticeable in the length of time required for chitin formation as shown in Table IV This table gives only the data on individuals upon which definite information was obtained

TABLE IV

INTERVAL BETWEEN INFESTATION AND CHITINIZATION

Fern No	No of scales observed	Interval (days)	Fern No	No of scales observed	Interval (days)
6	2	3 and 4 5	14	2	3
8	5	2 5	15	11	2
9	6	6	16	1	2
10	14	5	17	4	2
11	1	4	18	4	2 to 2 5
12	18	3	19	9	1 5 to 3
13	9	3 5			

Observations were made at daily intervals in each case The length of time is given to the nearest half day

At about the time that chitinization takes place the formation of the scale also begins This is a delicate, incomplete waxy covering over the posterior portion of the body and rarely covers very much of the insect The actual time of scale formation appears to be quite variable, but it usually occurs shortly after the chitinization It has been observed, however, several days after, at the same time as, and even a few hours before chitinization was visible

Moulting – Shortly before the time of the first moult the characteristic yellowish-white blotches begin to appear on the leaf just underneath the larvae

In moulting the nymph drops through the bottom of the old cast skin and grows out in a posterior direction Apparently, the mouth-parts grow out through the old mouth-parts and, as the coccid moves backward a little from under the exuviae, it pulls the old mouth-parts back with it (Pl XLVII, Fig 1) Thus the mouth-parts can be seen at the posterior part of the first exuviae

The time of the first moult varies considerably, being, I believe, prolonged by a high humidity (Table X) It varies between 13.5 and 21 days

TABLE X

DURATION OF THE FIRST STADIUM

Fern No	Days in greenhouse (high humidity)	No of scales observed	Average duration (days)
1–3	No scales established		
4	18	7	19.3
5	17	18	19.4
6	17	3	19.0
7			
8	17	6	19.1
9	17	4	18.0
10	17	6	19.0
11	17	1	19.0
12	14	12	19.6
13	14	5	18.8
14	13	9	16.9
15–18			
19	13	8	16.7
20 *	11	6	18.7
21	8	17	14.6
22	9	9	16.7
23	12	7	16.7
24	12	11	16.0
25	11	10	15.9

Sprayed with a nicotine spray on the 14th and 15th days

Mortality — The mortality during the first stadium was 10 8 per cent, 23 of the 213 larvae established on plants died These figures do not include, of course, the mortality previous to placing the larvae on the ferns There was a fairly high mortality here which probably is largely due to the handling of the insects during transference Of 535 larvae transferred, 95 (17 8 per cent) were found dead on the leaves on the following day These died probably as a result of the handling during transference Of the 38 6 per cent never recovered (see p 524) presumably the majority died without finding another fern frond on which to settle

Second stadium

Formation of scale — This takes place shortly after moulting, varying from a few hours to 1 day or even 2 days The female scale is laid down in layers by the insect as it swings the body in an arc of a circle, using the head end more or less as a pivot As it swings from side to side, it lays down a little layer of waxy secretion while it goes The color is usually a pale brown A thin, delicate ventral scale is also laid down at the same time, but is not very extensive

In the male, a snowy-white waxy secretion is emitted from three separate regions of the postero-ventral part of the body, one median and two lateral These are pushed out farther and farther until they come together on their lateral borders and coalesce, giving rise to the characteristic tricarinate appearance of the male scale

During scale formation, the larvae, especially the females, enlarge greatly, growing to the full second-instar size in 1–2 days, during which time the scale is completed

Ratio of sexes — The variation in scale formation immediately differentiates the two sexes which were till this time indistinguishable The observer is at once struck by the large predominance of males Of 190 larvae entering the second stadium, 143 (75 3 per cent) were males and 47 (24 7 per cent) females

Duration of female second stadium — The average length of the female second stadium is 13 days, but this may vary from

10 5 to 15 5 days inclusive Twenty-eight individuals were observed

Second moult — In the female the second moult is accomplished in much the same manner as the first and the mouth-parts are left in the same relative position

Male second stadium — The writer was unable to obtain any data with regard to the duration of the second and third stadia of the male It is probable, however, that the second stadium is about the same length as that of the female, since Comstock (1916) says of the male "Diaspinae" "The second moult is also synchronous with the second moult of the female

Third stadium

Male — As is usual in the Diaspidinae, the male goes through a third stadium, whereas the female enters directly into the adult stage from the second stadium MacGillivray (1921) states in his description of the Diaspidinae that the third stadium lasts only a few days This is probably true for *H aspidistrae*

Mortality during second and third stadia of male — While making examinations for parasitism from 5 fronds picked at random from a city greenhouse and 5 fronds from my stock plants, I kept a record of the male scales found unparasitized Of 113 such scales, 30 (26 5 per cent) had died during the second or third stadia The distinction between the two instars was rather difficult in some cases, since some were much shriveled For this reason they were grouped together Of the 56 larvae taken off the ferns and put in vials (cf "Technique," p 539), 37 5 per cent died during these stages Out of 28 larvae left on the ferns, 7 (25 per cent) died during the second and third stadia Thus it is seen that there is fairly high mortality at this time in the life-history

Adult

Formation of female scale – After the second moult the female insect lengthens out enormously and forms the scale at the same time This is accomplished in much the same manner as in the second stadium However, the scale in this case is much more extensive (Pl XLVII, Fig 1) The ventral scale is much larger also, extending over the whole area of the dorsal scale and thus inclosing the insect completely Plate XLVII, Figure 2, shows the relation of the insect to the first and second exuviae and the extent of the ventral scale When the scale is complete, the adult is wholly stretched out with its posterior end at the tip of the scale and the anterior end located under the posterior sixth of the second exuviae

Oviposition — One experiment indicated that parthenogenesis does not occur A plant bearing three healthy females was carefully examined and all males were removed At this time the females were in the late second stadium The plant was then isolated from all males in a box with glass sides When it was necessary to water the fern, the box was taken to another room where no ferns had been kept during the previous 6 months or more After 70 days in the adult stage, these insects were examined for ova None were laid under the scale, nor did any develop to any extent in their bodies However, the number of individuals used is too small to make the results anything more than suggestive

In the fertilized female the ova become noticeable about 8 days after moulting About the 12th day oviposition starts The writer has observed as many as 6 eggs laid by one female in one day The first eggs laid are placed at the extreme tip of the scale and, as egg laying proceeds, the adult retreats to a position under the exuviae Thus the oldest eggs are at the tip of the scale and the youngest up around the body During the time of oviposition a white powder is noticeable around the vulva of the female

The number of eggs laid by one insect varies greatly Counts were made of the number of eggs and empty chorions present under a fully mature scale (Table VI)

Emergence of male — Emergence takes place at night and is not very often observed, but the writer was able to see one partially emerge It died, however, when only half-way out This may have been due to the intensity of the light used to carry on the observation

One or two days before emergence a structure that looks like a straggly strip of wax is pushed out from the posterior end of the scale. This is really the cast skin of the third instar. It is quite evident that the male spends a short time under the scale before emerging, since the writer has dissected out a great many scales in which the adult insect was found. Evidently it stays under the scale until the wings collapse, dry and assume their final form, for I have found them in all these stages.

TABLE VI

EGG COUNTS

Specimen No.	Eggs laid	Specimen No.	Eggs laid
1	27	8	52
2	108	9	38
3	77	10	43
4	74	11	42
5	63	12	59
6	53	13	77
7	41	14	45

Maximum, 108 ova; average, 57 ova.

At this stage of their development mortality is high. Of 169 males dissected out, 50 (29.6 per cent) had died at this time.

When the wings are fully developed, the adult male starts to back out of the scale, as is shown in Plate XLVI, Figure 3. In doing this its whole body appears to expand and swell out as though it were filling itself with air in order to open the end of the scale more widely. Undoubtedly the legs help emergence greatly since they are moved about rather vigorously.

Longevity. — None of the males kept in vials lived through a whole day. Since they appear to be nocturnal in their habits, it is altogether likely that they live 12–18 hours in the adult stage under these artificial conditions.

The length of life of adult females differs a great deal. Apparently the fertilized females die shortly after they have laid their eggs, for the writer has found that in almost every case when a scale was filled up with eggs, the female was either nearly dead or had died and shriveled up Table VII gives a list of females dissected just before the conclusion of this work In this table a female is taken to be 'unfertilized" if she is mature and no eggs have been laid or are developing to any extent in her body "Longevity" here is used with reference to the time spent in the adult stage

TABLE VII

LONGEVITY OF FEMALES

Female No	Longevity when dissected * (days)	Condition when dissected	Number of ova laid
Fertilized			
1	82	dead	108
2	82	dead	77
3	63	alive	74
4	63	dead	63
5	60	alive	41
6	59	dead	53
Unfertilized			
7	82	dead	
8	70	alive	
9	70	dead	
10	70	dead	
11	68	alive	
12	66	alive	
13	66	alive	
14	61	alive	
15	58	dead	
16	55	alive	
17	55	dead	

* '*Longevity is given to the date of dissection, regardless of whether* the insect died before or not However data are given only on insects that either were alive at the time or had died just previous to dissection and had not dried up at all

Thus the average longevity of fertilized adults is 68 days and for unfertilized adults, 65 5 days

Average length of life

From data given in the preceding life-history, it will be seen that the average total life of the female is 90-100 days.

The life of the male is much shorter than that of the female. Only 6 males were observed to emerge as adults. Of these the average length of life was 37 days, the maximum length, 41 days, and the minimum length, 35 days.

V. BIOLOGICAL CONTROL

Aspidiotiphagus citrinus Cwfd., an endoparasite

Percentage of parasitism. – When the stock plants used in this problem were purchased in early November, it was noticed that a few scales had been parasitized by what was later found to be *Aspidiotiphagus citrinus* Cwfd., an aphelinid. As it was present in very small numbers, it caused no concern. By January 17, however, the parasitism had increased to 20 per cent. Finally, about the first week of March, the parasites became so numerous as to make it entirely impossible to complete any of the extensive spray program that had been mapped out. At the time of writing, the stock plant, which in the fall was heavily infested with scale, looked very healthy and had very few scales on it. This control was largely, but not wholly, due to the parasite. The percentage of parasitism is given in Table VIII. The first 5 fronds were taken from the author's stock plants. They were not fumigated at any

TABLE VIII

PARASITISM BY *A. citrinus*

Frond No.	Scales examined	Percentage parasitized	Frond No.	Scales examined	Percentage parasitized
1	55	58.1	6	56	28.6
2	50	61.8	7	52	75.0
3	103	60.2	8	16	6.2
4	104	76.0	9	51	68.6
5	37	67.6	10	13	46.1

time during the previous 5 months The other 5 were picked at random from infested ferns in a city greenhouse, where a more or less regular fumigation program was maintained Parasitism was recorded only when the effect was externally visible

From Table VIII it can be seen that the percentage of parasitism may become quite high and thus this aphelinid is an important consideration in the control of the scale

Oviposition — This minute hymenopterous insect can often be seen walking over the fern leaves, with its antennae tapping away as it goes along When it comes to a scale of *H aspidistrae*, it taps around the edge of it and then squats on the center of the scale and the ovipositor is thrust down from its hidden position under the body Oviposition lasts from a few seconds to 10 minutes Male and female coccids are parasitized with equal readiness

Emergence — Previous to emergence, which is very interesting, the insect lies inside the integumental case of the dead scale, with the head of the parasite toward the posterior end of the scale and the ventral side toward the dorsal part One parasite that had just completed the pupal stage was watched with interest First it cleaned its legs and antennae After this it began to feel around with its mouth-parts, evidently looking for a place to bite through A large hole was started from a series of little holes placed in a circle and then joined by cutting away the intervening material, which was taken off in little strips along the edge of the hole As each strip broke off, the insect ejected it from its mouth to the outside of the scale After feeling all around the edge of the hole to make sure that there were no projections and that it was large enough, it started to emerge First the head and antennae appeared and then the first legs, followed rapidly by the second and third pairs Immediately after emerging it crawled briskly away

No males were noted among the comparatively few individuals observed

VI ARTIFICIAL CONTROL

Extensive experiments on sprays were planned by Professor J W Burns and the author, but, on account of the heavy inroads by the parasite, the program had to be abandoned The following compounds were suggested by Professor Burns as possible sprays when combined with nicotine and soap (1) glycerine, (2) methyl borate, (3) ethylene glycol, (4) ethylene chloride, (5) ethylene chlorohydrin, (6) acetylene chloride These compounds all dissolve insect wax rather freely and thus, combined with nicotine and in the proper proportions, should be effective

In one case a spray consisting of nicotine, soap and water was applied to an artificially infested plant while the insects were in the late first instar Apparently it delays the moulting, as is shown in fern No 20, Table V

Another factor in artificial control is the maintenance of a high humidity, since it appears to prolong the life-cycle of the scale and thus decreases the rate of reproduction Gibson and Ross (1922) state, in reference to *H aspidistrae*, that "this insect is of no importance in humid fern houses, and only becomes troublesome on plants kept in a dry atmosphere, such as one finds in houses, stores and halls"

Removal of the branches infested to the greatest degree would also help greatly, as was demonstrated in the case of the stock plants already referred to (p 533) The cutting of these fronds caused the plant to send out a lot of healthy new ones and got rid of a large number of the scales at the same time

Finally, anything that can be done to better the general health of the plant should prove a great aid in the control of this scale, since it will encourage an abundant growth of new fronds, thus permitting the constant removal of older ones which are the most heavily infested

VII TECHNIQUE

Mounting of scales

The method of mounting used by the author was that described by MacGillivray (1921) This consists of clearing the coccid in potassium hydroxide, either by the fast method (boiling) or by the slow one (allowing it to remain 24 hours in cold solution) It is then washed in distilled water and finally in acidulated water (1 c c hydrochloric acid to 99 c c distilled water) After this, it is stained in *Säuerfuchsin* for 20 minutes, dehydrated in 95 per cent alcohol for 15 minutes and cleared again in carbol-xylol or oil of cloves, preferably the latter Finally it is mounted in Canada balsam

The writer found that the handling of a large number of females was facilitated by placing them in a small, fine-meshed wire basket In this way they could be transferred from solution to solution with the least handling

Males, first instars and other specimens small enough to go through the wire mesh were usually handled by the slow method To do this, they were first placed on the slide on which they were to be mounted Several large drops of potassium hydroxide solution were added, and the slide was put in a Petri dish with a moist blotter in the bottom The dish was covered and left overnight By this method a high humidity was maintained and very little evaporation took place While they were being immersed in alcohol, a small watch glass containing alcohol was put in the Petri dish in place of the moist blotter This maintained a high alcoholic vapor pressure and again reduced evaporation to the minimum

Handling of ova

The eggs were dissected out from under the adult scale with the aid of a binocular microscope The upper surface of a rectangular piece of balsa wood was covered with a piece of cross-section paper, cut to fit, and the whole was wrapped with a small piece of cellophane, a glassy paper often used in wrapping chocolate boxes It gives a squared surface on which the number of eggs can be accurately counted, if this is desired, and also permits the pinning down of the fern leaflets during dissection At the same time it gives a smooth surface from which the eggs are easily removed with a camel's-hair brush

At first these ova were pasted on small cards, but any of the larvae that hatched seemed to be stuck in place or did not emerge properly Similar results were obtained when the ova were placed on glass plates Finally, eggs were successfully incubated by making wax plates in Petri dishes These were made in much the same manner as are agar pour plates in bacteriological technique

The plates were ruled off in squares to facilitate a thorough search of the wax surface The cover of the Petri dish was lined with a moist filter paper Ova were placed on the wax plates and incubated at 70° F The plates were looked over thoroughly each day and the crawling larvae transferred to ferns as described later Usually, about 100 per cent humidity was maintained Moisture condensations, if not too extensive, helped to confine the larvae and prevented them from crawling up the side of the plate It was found that, if the plates were put under an electric light shortly before examination, hatching was apparently hastened

Experimental plant infestation

The problem of securing artificial plant infestation occupied about two months It was finally found that the greatest care had to be taken in handling young larvae and the host fern until they had all settled down The following technique was worked out Small ferns with from one to three fronds were used in all the experiments involving artificial infestation The plant was first thoroughly examined for signs of scale and then brushed with a camel's-hair brush, especially along the stem, to remove all débris which might later obscure the view A cradle made of soft lens paper (Pl XLVIII, Fig 1) was now tied on the under side of the frond so as to include the part to be infested and the fern was turned on its side under a binocular microscope

The transfer from the plate to the fern was the next problem that confronted the author At first, paper points about two inches long were used The point had a tendency to fray, however, if it became moist, which caused the insect to stick to it Waxed paper was used next, and, though it was an improvement, the same trouble was encountered Finally, cellophane was used and proved very efficient. The larvae did not very often fall off in transit from plate to fern and yet the writer had no difficulty in placing them on the frond A wooden handle was attached to the pointer to prevent curling due to the heat of the experimenter's hand In this way the larvae were picked off the waxed plates and placed on the frond It should be emphasized that the greatest care must be taken not to jar the fern in handling it, until after the larvae have settled

On the following day the fern was examined and a record made of the positions of the larvae To do this, a binocular microscope was mounted as is shown in Plate XLVIII, Figure 3 This method of mounting permitted movement of the binocular in any direction and tilting to any angle In order to overcome the necessity of changing the position of the light each time the binocular was moved, it was clamped to the body tubes of the binocular and thus focused automatically on the fern The light used was an ordinary substage illuminator with the daylight glass removed and a watchmaker's lens inserted in place of it This lens happened to have about the same focal length as the binoculars The illuminator is also shown in Plate XLVIII, Figure 3

Labeling of plants

In order to keep a record of each specimen, ordinary cardboard tags were used Both faces of each tag were divided longitudinally by a median line and transversely by an upper and a lower line Above the top horizontal line, the side of the frond was indicated, i e upper or lower side Below the lower horizontal line the number of the tag was placed The space between the horizontal lines was divided according to the number of leaflets intended to be included in that particular tag, the vertical line being used as the stem Where more than one scale had settled on a leaflet, the numbers were grouped together, e g if one leaflet bore 7 on one side and the number of larvae already recorded from previous plants was 99, then the 7 would be recorded on the tag, not as 99, 100, 101, etc , but as 99–105 In this case the insect nearest the stem would be given the lowest number, i e 99, and the next one would be the next lowest number (100), and so on Thus the numbers increase from the stem outward When 2 scales were vertically one above the other, the upper scale was designated by the lower number Thus the upper one would be number 101 and the lower, number 102 When insects were located on the stem, an arrow pointed to the stem (as represented on the tag) from the numbers, and the same rules applied as regards the position of scales one above the other An asterisk marked the leaflet upon which artificial infestation was made The tags were placed on the stem of the frond just below the lowest leaflet included in the tag

Observations on moulting and oviposition

Since the insect spends the final stages of its life under a scale, observations could no longer be carried out directly, as was done in the earlier stages It became necessary, then, to direct a light through the fern leaflet and scale, a method that obtained a silhouette effect To do this, apparatus was set up as in Plate XLVIII, Figure 2 The light was another substage illuminator in which a small lens (linen tester) was substituted for the daylight glass It was not arranged so as to shine directly up into the binocular, but was set at an angle so as to prevent too much eye strain With this method, insects that had not secreted too dark a scale could be observed Very dark scales prevented all observations except by dissection

Handling of Males

Since it was known that the males would not derive any nutriment from the fern leaf shortly before emerging, they were taken from the ferns at this stage and put separately in small vials properly labeled These were kept in racks in a dark box in the incubator at night in an effort to simulate normal conditions, since the incubator light would be on most of the night During the day they were exposed to daylight Not very much success attended this method because only 6 of 64 males treated in this way emerged However, the high natural mortality during these stages, as stated before, must also be taken into consideration here

VIII SUMMARY

H aspidistrae, a pest on Boston ferns in particular, spreads rapidly from fern to fern, probably by means of crawling or by being jarred and dropping For this reason, greenhouse proprietors should be careful to isolate infested plants thoroughly

The average life-history of the female extends over a period of about three months and that of the male, slightly more than one month

The control of this scale depends upon several factors

1 Presence of the parasite, *Aspidiotiphagus citrinus* Cwfd
2 Maintenance of a high humidity in the fern house
3 Preparation of a suitable spray
4 Constant trimming off of badly infested fronds
5 Optimum growing conditions of the fern This makes factor 4 feasible

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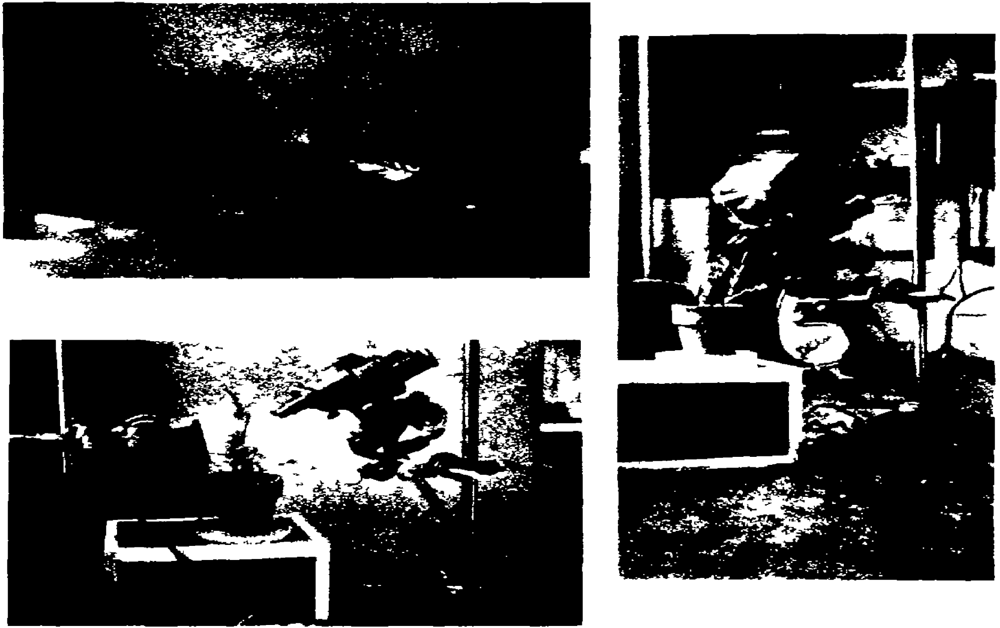

Fig 2

PLATE XLVII

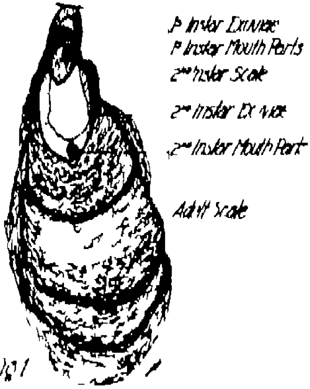

Fig 1

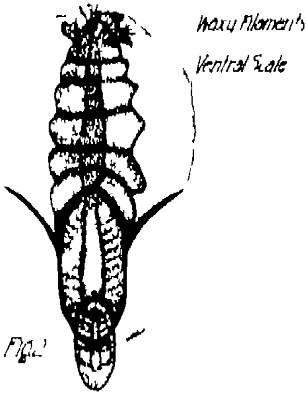

Fig 2

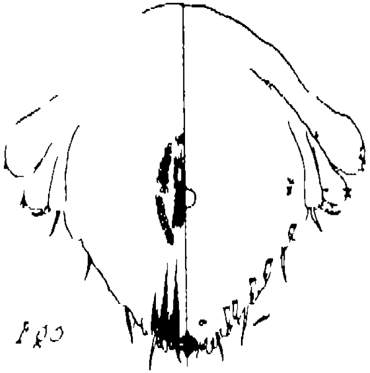

Fig 3

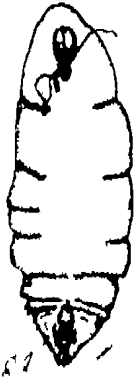

Fig 4

PLATE XLVI

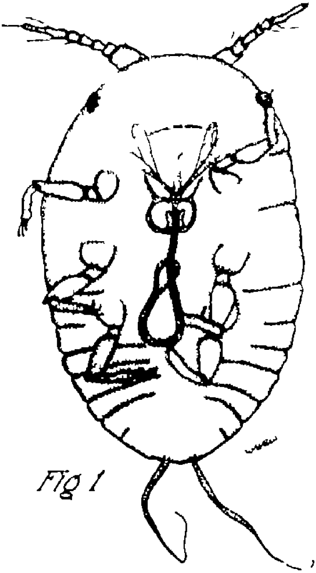

Fig 1

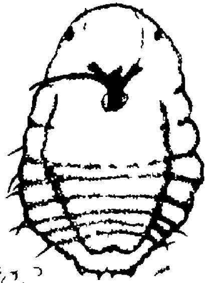

Fig 2

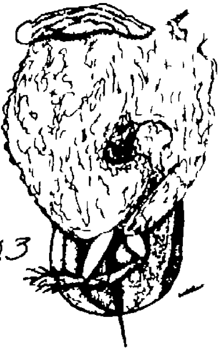

Fig 3

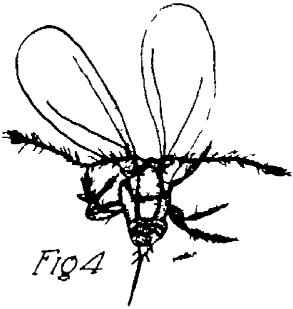

Fig 4

EXPLANATION OF PLATES XLVI–XLVIII

PLATE XLVI

FIGS. 1–4 *Hemichionaspis aspidistrae*
(Figures are drawn to different magnifications)

FIG 1 First-instar larva, ventral aspect

FIG 2 Second-instar male, ventral aspect

FIG 3 Adult male emerging from scale, ventral aspect

FIG 4 Adult male, dorsal aspect

PLATE XLVII

FIGS 1–4 *Hemichionaspis aspidistrae*
(Figures are drawn to different magnifications)

FIG. 1 Scale of adult female

FIG 2 Exuviae and ventral scale, showing the position of the adult in relation to them

FIG 3 Pygidium of adult

FIG 4 Adult female ventral aspect

PLATE XLVIII

FIGS. 1–3 Apparatus for artificial infestation of ferns with
Hemichionaspis aspidistrae

FIG 1 Small fern with lens paper cradle attached preparatory to artificial infestation

FIG 2 Apparatus set up for observation of second instar and adult insects under their scales

FIG 3 Apparatus for observation of young crawling larvae

A CONTRIBUTION TO THE BIOLOGY OF SIMULIUM (DIPTERA) *

YI FANG WU

INTRODUCTION

IN THE earlier attempts to study Simulium larvae in the laboratory, it was claimed that in standing water they would die within a very few hours Since death occurred too quickly to be due to food reduction, the cause was supposed to be a deficiency of dissolved oxygen This phenomenon, together with the natural occurrence of the larvae in swiftly running water only, was interpreted as indicating that their oxygen requirement was very high In fact, it has long been assumed and frequently stated that the restriction to running water is due wholly to so high an oxygen demand that only the much-agitated water of a swift current would provide suitable conditions for these larvae Though this explanation seemed plausible, no experimental study has ever been made to test it This paper is the result of an attempt to study the influence of the factor or factors involved in the running-water habitat and to ascertain whether or not oxygen is the sole determining agent, as heretofore supposed Contributions have likewise been made to the knowledge of the general biology and life-history of these black fly larvae and are presented in Part I

This investigation was carried out mainly at the University of Michigan Biological Station All streams in that region were examined, but intensive study and the experimental work were done in Carp Creek, Maple River and Bessey Creek Some of the laboratory experiments were performed at Ann Arbor with material collected from the Huron River

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* Contribution from the Zoölogical Laboratory, University of Michigan and the University of Michigan Biological Station

ACKNOWLEDGMENTS

This investigation was done under the supervision of Professor Paul S Welch, to whom the writer wishes to express her sincere thanks for his kind interest in the problem and helpful criticism during the progress of the work She is also indebted to Professor George R La Rue, director of the University of Michigan Biological Station, for the use of the facilities at the Station, and to Mr Frank E Eggleton and Mr Ralph S King for help in the preparation of equipment

PART I GENERAL BIOLOGY

EGGS

Description

The egg of Simulium is generally described as elongate-oval (Malloch, 1914, p 3) or as triangular with rounded angles (Pomeroy, 1916, p 11), but examination of the eggs of *S vittatum* Zett and *S venustum* Say showed these descriptions to be based upon two different views of the same egg One side is somewhat flattened, but the opposite one is humped, the highest point being a little nearer one end The shape is triangular when so viewed, but if the egg lies on the flattened side and is viewed from above, it is rather oval with both ends broadly rounded Measurements of the egg of *S vittatum* are length, 0 25 mm , breadth, 0 15 mm , height, 0 14 mm Those of *S venustum* are length, 0 23 mm , breadth, 0 14 mm , height, 0 13 mm Eggs of both species have tough shells and are attached to the support by means of a transparent sticky substance, which remains elastic in alcohol and can easily be taken off the egg

The arrangement of the eggs in the mass differs in the two species studied Eggs of *S venustum* are, as generally described, placed irregularly in a compact mass (Johannsen, 1903, p 344, *et al*), which may be several layers thick Those of *S vittatum* are deposited in a string which curves or twists over itself and in which the eggs are laid in a single row, mostly side by side, but sometimes end to end When oviposition is heavy and the egg-mass becomes extensive and several-layered, the string arrangement may not be apparent, yet the mass still does not appear compact

Location

Eggs of *S venustum* and *S vittatum* are deposited on leaves of aquatic plants, stones, logs and other objects in the stream They are usually at or near the water-level Occasionally some are found above water on vertical objects or on the upper surface of a log or a stone Garman (1912, p 20) recorded this unusual occurrence in a general statement "The eggs were found placed on rocks on the banks a few inches above the surface of water" From observations made in Bessey Creek and Maple River, this position may be due to one or both of two causes operating subsequent to oviposition (1) fall in level of the stream, and (2) growth of the supporting plant Stones in Bessey Creek had egg masses on the upper surfaces just at water-level, but a few days later the same stones were half out of water, with the eggs drying or kept moist by the wavelets As for eggs laid at the water surface on a vertical emergent plant, it is obvious that growth of the basal regions of the plant would carry them out of water Such an egg-mass generally had the appearance of a series of bands of different colors, the topmost one being the darkest and the lower ones grading down to lighter shades This indicates that the eggs at the various levels were of different ages, with the oldest ones highest and those newly laid nearest to the water Eggs deposited at water-level on different days were carried successively out of water as the plant grew taller This observation and the fact that oviposition on land has never been recorded indicate that the eggs which Garman found were not deposited on the bank, but were probably left stranded on a plant because of a fall in level of the river.

Development and hatching

At oviposition eggs are creamy white, then gradually change to light tan, brownish tan, brown and finally blackish at hatching All which develop normally have a shiny appearance, occasionally some fail to develop and remain dull whitish As the general color becomes medium tan, the pointed end of the egg appears darker and the head of the embryo larva can be seen. A day or two before hatching, eye-spots become visible The egg-burster is indicated by a dark spot in the middle of the head, as described by Puri (1925, p 329)

The emergence slit in the egg-shell invariably occurs at the broad end After the head pushes out of the opening, the proleg is applied to any adjacent object, securing temporary anchorage, and the rest of the body soon follows The general shape of this larva is cylindrical, with the head comparatively large and the abdomen short The larva is immediately active and moves about in a characteristic manner After a few hours the body assumes the normal form of the older larvae

Eggs develop normally when kept in still water or in a damp bottle in the laboratory In the field, eggs have been found to develop in *the absence of definite current* or in air above water-level For instance, in the calm protected conditions of Maple Cove, Douglas Lake, eggs and patches of egg shells often occur on the emergent water plants 20 to 70 feet from the shore As already mentioned, egg-masses may be left out of water owing to the fall of river level or growth of the supporting plant All that were kept moist by wavelets and capillary action develop normally Possibly this explains the statement by Bishopp (1912, p 384) "Eggs are placed on various objects just above the water level They hatch and the young larvae enter the water" Barnard (1880, p 191) made a somewhat similar observation, and stated that the small larvae issued from eggs on the sloping rocks a little above water, and that "from these the young were passing downward into the water to begin an aquatic life"

Incubation period

In natural habitat — The incubation period for *S vittatum* was 4–5 days in the latter part of June and through July when the temperature of the water was about 20°–22° C In order to secure eggs of known age, fresh cat-tail leaves were bent to float at the water surface Oviposition usually took place in the late afternoon, and on the next day the leaves bearing the fresh eggs were tied to a stake to keep them well submerged and thus prevent further oviposition By observation of them until hatching their definite incubation period in the natural habitat was obtained Pomeroy (1916, p 12) recorded the minimum period of 7 days and the maximum of 12 days in South Carolina from June to October, but did not state whether it was observed in the natural habitat or under laboratory conditions

In standing water — The incubation period in standing water was found to vary greatly, viz , from 5 to 55 days Several experiments confirmed this statement Hence the time required in standing water was found to be much longer than in the natural habitat The incubation periods of the various eggs in the same mass differed, those in the top layer generally hatched earlier than those beneath, although the lower layers had been laid first

Resistance to desiccation

Edwards (1920, p 240) suggested that probably *S latipes* Meig passes the dry season, when the streamlets are dry for the greater part of the summer, in the egg stage, and Cameron (1922, p 15) from circumstantial evidence proposed that *S simile* Mall probably overwinters in the egg stage The writer subjected *S vittatum* eggs to various periods of desiccation in the laboratory and then submerged them in water A very small number hatched from the egg-mass that had been exposed to the air for 10–14 hours, but not a single hatching occurred from the eggs that had been out of water from 18 hours to 5 days Evidently *S vittatum* eggs cannot resist desiccation Field observations support this conclusion When, for any reason, eggs were exposed above water, only those that were kept moist hatched Others beyond the reach of wavelets appeared dry and shrunken, and failed to hatch when returned to water

LARVAE

Duration of larval period

The larval period of *S vittatum* was studied in Maple River during the month of July when the variation of the water temperature was 18°–26° C (mostly 20°–23° C) Fresh cat-tail leaves were bent down so that they were slightly submerged and parallel to the water surface Deposition of eggs and the hatching were recorded, and examination of the larvae was made every second day Growth was found to be very rapid and the larval stage, for the majority of each brood, lasted only 13–17 days

Emery (1913, p 331) found the larval period of *S vittatum* to be about two months and three weeks This result was not based on observation of the larvae, but was merely an estimate from the number of broods This method seems very faulty because the adults appear throughout the summer and it is inaccurate to distinguish the different broods of larvae merely by the relative abundance or scarcity of the flies on the wing Puri (1925, p 300) obtained the larval duration of two British species by rearing them in the laboratory This is a very accurate method for determining the length of the period in aquaria, but it does not necessarily follow that the period is the same in the natural habitat

In Carp Creek, where *S venustum* was the predominating species, the larval period was much longer This was probably due to two factors, namely, the low temperature of the water (10°–14° C in the summer) and the scarcity of plankton organisms Observations on this point were made in connection with the trough experiments described in the experimental section The colonies transplanted into the experimental current troughs usually consisted of larvae of different ages, and they pupated throughout the whole observation period of seven and one-half weeks At the end of this period there were still some larvae left These troughs were examined every other day and the larvae were closely observed, so that it is certain that they were all of the original transplanted population Since the early history of the larvae was not known, the definite larval period could not be determined in this way, yet from the record it is clear that it could be longer than seven and one-half weeks in the summer months It should be added that, although the observations were made under experimental conditions, the water was from the natural habitat and the current was of various velocities. McBride (1870, p 227) recorded the larval period of *S venustum* to be about four weeks during the warm season, but did not give the temperature of the water

Habits

Attachment — The larva is attached by means of the posterior disk, which is provided with rows of hooks arranged in a circle That this mechanism is not a sucker, as was formerly supposed, was shown by Tonnoir (1923, p 164) Attachment to the support is accomplished by means of a glutinous material which issues from the mouth and to which the disk is brought in the looping movement

In experiments on current rates, it was found that the larvae were still well established in a velocity of 6 feet per second This shows that the attachment must be very firm to resist the pull of such high velocity Occasionally, dead larvae were found attached to the support, showing that this adherence continued to be effective even after death

The angle of the body with the support diminishes as the current rate increases In a moderate current the larva stands semierect, but with increased velocity the angle becomes less and less until the body lies almost prone upon the support This is very apparent on the more or less vertical surfaces of logs and boulders, on which the larvae are established in waterfalls

Locomotion — The looping movement of the larva was described in detail by Tonnoir (1923, p 104) and by Puri (1925, p 297) Observations of the writer agree with those of Puri Besides the regular mode of locomotion, the larva is able to make some progress by means of only the mouth-parts and the proleg, with the abdomen remaining straight and unattached The process of climbing on a silk thread was often observed When the larva was on a strand of several silk threads, it either climbed in the regular fashion with the proleg and mouth-parts, or applied its posterior disk to the strand and proceeded with a looping movement

Food

Being sedentary and provided with a mechanism for straining small particles from the water, the larva does not seem to be selective in feeding, but takes whatever the fans can catch as the current passes through them Examination of the stomach contents confirmed this general conclusion. Larvae from Maple River contained mostly diatoms, which were very numerous in the summer plankton population of the lake water, but those from Carp Creek had few diatoms and much material that could not be identified, such as bits of plant tissue and other débris

In the standing water cultures, a few larvae were observed feeding on the deteriorating bodies of dead larvae Occasionally larvae used their mouth-parts to scrape materials from the substratum This behavior may have been caused by the unfavorable conditions in the standing water

Parasites and enemies

Larvae of *S hirtipes* Fries from Huron River, near Ann Arbor, were parasitized with a nematode, probably *Mermis*, which Strickland (1911, p 302) found in the same species in Massachusetts Larvae of *S vittatum* from Maple River were occasionally infested with a protozoan parasite Examination of the fresh material showed that the spores and sporoblasts correspond closely with the figures given by Strickland (1913, p 97), and the appearance of the parasitized larvae also agreed with his description

In an aquarium containing *S jenningsi* from Huron River, a *Chironomus* larva was found to attack the Simulium larvae. It seized the side of the living victim with its mandibles and began feeding on the soft tissue It was seen to kill several larvae, but this might be caused by the absence of other food, it does not prove that Chironomus is a natural enemy of Simulium

PUPAE

Duration of pupal stage

The duration of the pupal stage has been reported differently by various authors. The longest period given was three weeks for *S venustum* Say (McBride, 1870, p 366) and *S pictipes* Hagen (Coquillett, 1898, p 67) But both were mere estimates of the interval between the first appearance of pupae in the breeding place and that of the adults on the wing Results of direct observation were given by the following investigators Newstead (1907, p 40), 2–6 days for *S ovatum* Mg , Pomeroy (1916, p 25), minimum period of 3½ days and maximum 9 days for *S venustum* Say, Cameron (1922, p 15), 5–7 days for *S simile* Mall , and Puri (1925, p 302), about 5 days in the summer and longer periods at lower temperatures for *S nolleri* Fried Though these workers indicated the temperature conditions, they failed to state whether their observations were made in the natural habitat, in breeding aquaria, or in the damp chamber recommended by Newstead for rearing adults from pupae

A careful study of the duration of individual pupal stages was made in connection with a trough experiment Although carried out in the aquarium building, it was in fact comparable to normal conditions, because the stream in the trough was of unmodified lake water and had a velocity of about that of the natural habitat The V-shaped wooden trough, 54 inches long, was set up with an incline to secure the required velocity Water was supplied from the large reservoir tank, which was kept filled with fresh lake water by a power pump Larvae of *S vittatum* from Maple River were transferred into the trough They became well established on the sides and gradually pupated Examination was made three times a day and later twice daily after the majority had pupated and emerged At each examination all the newly transformed pupae were sketched on the board above the water line and each was assigned a number, later the emergence was recorded according to the numerals Thus the duration of the individual pupal stage was obtained The temperature of the water for the first ten days varied between 18° and 21 6° C After this the average temperature of the water fell 1½ degrees, but only 7 per cent of the pupae were left in the trough Altogether 101 larvae pupated Ninety-one completed development, of the other 10, 7 died, 1 was removed for examination, 1 was lost, and 1 had not emerged when the experiment was discontinued The curve plotted from the resulting data shows a prominent mode at 4¼ days, with a minimum period of 3¼ days and a maximum of 5¼ days. The total variation is 2 days, but 66 per cent have a variation of only one-half day, their periods being between 4 and 4½ days. Of the rest, 16 per cent fall between 3¼ and 3¾ days and 17 per cent between 4¾ and 5¼ days (with 5, 9, 10 pupae).

Cocoon-spinning and pupation

Spinning of the cocoon.—Before the larva actually starts spinning, it performs a series of preliminary motions: it bends back and applies the mouth-parts to a certain point on the support near its posterior end, then suddenly pulls its head away with some force. It repeats this performance many times, testing various areas around itself on the supporting object. In one instance this was observed to last for more than one minute. The purpose of this behavior appears to be the cleaning of the ground of débris, or the testing of the firmness of the substratum.

The process of cocoon-spinning was fully described by Tonnoir (1923, pp. 165–169) for *S. tillyardi*, an Australian species, whose cocoon is almost exactly circular. Puri (1925, p. 301) gave a brief account of three British species whose cocoons are of the wall-pocket type. The writer has studied the spinning of *S. venustum* Say, but found it to differ from Puri's description in that the larva never changes its attachment throughout the whole process. This point agrees with Tonnoir, although the *S. venustum* cocoon is not circular, but like a wall-pocket. Firmly anchored by means of its posterior disk, the larva bends back and places a loose network of silk on the supporting object just posteriorad to its point of attachment. Then it works forward along the side of the body, until the bend is at about the anterior third. After fixing the silk to the support it twists so as to turn the ventral side outward and upward, and produces a strand of silk while describing an arc dorsally over its body to a similar point on the opposite side. Repetition of this movement results in the formation of the rim of the future cocoon. Since the larva does not change the point of attachment, the two ends of this arc are in fact the extreme points, in front, to which the larva can reach when bent at its anterior third The limit to which it can stretch behind naturally becomes the apex of the case With these three points fixed, the larva spins more threads along the sides and dorsally over its body, and the cocoon soon takes definite shape Then it spends some time working over the closed end of the cocoon It takes from 50 to 60 minutes to complete the whole process The network which is put down at the beginning becomes the floor of the posterior part of the cocoon, the anterior margin of which marks the place where the larva is attached while spinning, and this explains why the front of the cocoon has no bottom

Process of pupation The pupation process was found to be quite similar to that described by Tonnoir (1923, p 169) Doubled into the form of a U, back to back, the larva rotates for from 10 to 15 minutes A slit occurs along the lateral and the posterior borders of the fronto-clypeus and continues ventrad between the head and thorax The gill filaments emerge, the head capsule shell comes off the front, and the rest of the larval skin is cast from the posterior end as the pupa withdraws from it and straightens out inside the cocoon For a few minutes slight sidewise wavy movements continue in the posterior region By the time the pupa comes to rest mouth-parts and wing pads are already traceable

In standing water — Pupation in standing water was observed many times Numerous individuals fail to come out of the larval skin and die with only the thoracic region enlarged and gill filaments bursting out at the sides Some may complete pupation, but with no cocoon or only a shapeless mass of silk threads Others build their cases and pupate in the normal manner The only difference between such a pupa and one formed in running water is that the gill filaments in the former spread out in all directions, while those in the latter lie rather straight in the direction of the current

Movements of pupa

Turning within cocoon -- Inside the cocoon the pupa is able to move or turn rather freely Pupae have frequently been seen on the side or with the ventral surface upward The most active motion observed was when a pupa was disturbed by a neighboring full-grown larva clearing the ground for cocoon-building. When the larva touched the anterior end or the gill filaments of the pupa, the latter performed the avoiding reaction with its anterior region

Desertion of cocoon — McBride (1870, p 366) observed that the pupa of *S venustum* loosened itself from the case a day or two previous to emerging Puri (1925, p 301) claimed this to be wrongly described, because "once a pupa has entered the cocoon, it is fixed to the latter and never leaves it of its own accord" Though this is the normal course, the writer has, however, observed pupae, some of which transformed later, leaving their cocoons under distinctly unfavorable conditions Emery (1913, p 336) recorded a similar observation, but did not give details However, the statement that they "faced in the opposite direction alongside of the cases" indicates that they could not be under normal conditions

Enemies and parasites

A Chironomus larva was observed attacking pupae in an aquarium It penetrated the side of the abdomen and fed on the soft tissue inside, leaving the pupal skin clean and intact In the field no such empty pupal skins have been found, but dead pupae were occasionally encountered, most of which had a puncture in the thoracic or abdominal region while the internal tissues were in various states of deterioration It has not been ascertained what enemy attacked them

Dissection of pupae yielded no evidence of parasites The only record of parasites in Simulium pupae was given by Enderlein (1921, p 198), who obtained two braconids belonging to two subfamilies from a group of 15–20 pupae He stated that this was the only time he obtained parasites, although he had reared thousands of Simulium flies from pupae

Emergence

Process of emergence — The process of emergence was studied in the natural habitat and in the aquarium The pupa appears silvery, owing to the presence of gas underneath the pupal integument The relation between gas accumulation and the splitting of the exuviae is not known, although it was found that pupae may manifest the silvery appearance for more than one hour before the splitting occurs As soon as the split along the mid-dorsal thoracic region takes place the adult thorax is exposed under a layer of silvery gas Then the slit extends between the head and thorax and along the lateral margins of the front piece covering the vertex of the adult fly Gradually more of the thorax comes out, carrying with it the head, which is still bent, facing downward, and does not assume the normal position until it is all free from the pupal skin At the same time an undulating movement goes on in the abdomen After the head and most of the thorax are free, the fly comes up faster — the direction is more vertical than forward — until only half, or less, of the abdomen is still inside the pupal skin It takes the fly 2–4 minutes to come out so far, then it rests for about one minute Throughout the whole period the fly has not struggled any in emerging from the skin, during the interval of rest it may remain perfectly quiet, or the front end may wave slightly and slowly sidewise Then it begins to come up again, as soon as the front legs are free and wriggling, it is immediately carried upward in the gas envelope, and on reaching the surface flies away at once Cameron (1922, p 16), Coquillett (1898, p 67) and Pomeroy (1916, p. 26) also found the adult to take flight almost immediately upon coming up to the surface of the water If, according to certain other workers (Emery, 1913, p 337, McBride, 1870, p 356), it stays on the surface for the wings to dry, the current must be moderate, otherwise it would be carried downstream and possibly suffer accident

Emery (1913, p 337) gives an account of emergence of a pupa on a stone when held up in the air This should not be taken for the normal process under water, for the buoyancy of the gas coming off the fly renders the condition quite different According to the observation of the writer, the fly never exerts any "pulling", and after the thorax is out, it is only by having part of the abdomen and tips of the legs still inside the pupal skin that rise to the surface is delayed It has not been observed to pull out its legs until ready to come up with the gas envelope

Emergence in air — Newstead (1907, p 40) reared adults by keeping pupae in a damp chamber Flies are thus able to emerge in air as well as in water Pomeroy (1916, p 25) noted the fall in river level, leaving the pupae exposed to air, and added that they would emerge even after having been 24 hours out of water if the adult is sufficiently developed Recently Pulikovsky (1927) studied the respiratory adaptation of Simulium pupae and called the pupal gills "amphibian" in nature, because they function as respiratory organs both in water and in air His work was on a species inhabiting mountain streams that dry up easily From one of his experiments (p 418) he concluded "Die Puppe verlangt am Anfang ihrer Entwicklung notwendigerweise die Gegenwart von Wasser, weiterhin fällt diese Notwendigkeit fort (trocken gewordene Puppen sind entwicklungsfähig)" It seems to the writer that there are other factors to be considered besides the degree of development itself Since pupae are able to develop normally when removed to a damp chamber even immediately after pupation, it proves that submergence is not indispensable for early development The really significant factors, it seems to the writer, are (1) the humidity of the surrounding air, and (2) the degree of chitinization of the pupal skin The newly transformed pupa is pale in color, and as chitin is deposited it gradually changes to tan, light brown, and finally black when the fly inside is fully developed and shows through the pupal skin If the surrounding air is humid, development is not affected, even when the pupa is not protected by a well-chitinized integument But when such a pupa is subjected continuously to dry air, it may be that the tissue inside loses water through evaporation and becomes too dry for normal development When the pupa is advanced in development and protected not only by its own chitinized integument but also by that of the future fly, the dry air will not do any harm

The writer has studied pupae above the water-level in natural habitats and pupae that were kept dry, experimentally, for various periods On vigorously growing cat-tail leaves in Maple River, pupae were occasionally found from 1 to 10½ inches above water

These were in different stages of development and the cocoons were almost invariably dry Of 45 pupae observed, 34 produced imagoes, 4 were lost from the leaves, and 7 died Four of the dead were very dry and shrunk into the cocoon, and 3 showed the thorax of the fly partly projecting through the emergence slit and appearing dry also Excluding the 4 that were lost, this record shows a mortality of 17 per cent apparently due to dryness In the laboratory pupae on their natural support were exposed to the air for different lengths of time and then put into damp chambers Of 21 pupae so exposed for 24 hours, 17 emerged and 4 dried up Of 6 others exposed for 34 hours, 4 black and brown pupae emerged and the 2 tan ones became dry Of 6 additional ones exposed 54 hours, only 1 emerged and that within a day, showing that it was advanced in development when subjected to desiccation Ten pupae remained in the dry air, to which they had been exposed for 54 hours Of these not a single emergence occurred From these results it is evident that there is a desiccation limit beyond which the pupae are unable to complete development

Pupae in standing water

The writer has found that most of the pupae kept in standing water failed to complete development This was true of pupae collected from the field and of those that pupated in standing water

IMAGO

Duration of the adult stage

Since it was impossible to make direct observation on the duration of the adult stage in nature, flies have been studied only in captivity Friederichs (1921, p 83) succeeded in keeping the flies alive longer than other investigators did He reared *S maculatum* Meig on sugar solution in a very large cage and had 2 females that lived 23 days, the majority died within 14 days Blacklock (1926 a, p 12) experimented with *S damnosum*, and only 1 out of 268 lived for 10 days, the majority dying within 4 days

The writer, working on *S vittatum* and *S jenningsi* Mall, used sugar solution, soaked raisins or water alone For 52 flies supplied only with water, the longest period was 6 days for 1 female The majority died within 3 days, 5 males and 5 females lived for 5 days When sugar solution or soaked raisins were provided as food, the period was greatly lengthened Both males and females were seen to feed on it The longest period obtained was 18 days for 2 males and 3 females of *S vittatum* and for 2 females of *S jenningsi* The majority died within 8 days, but there were individuals that had a period varying from 9 to 17 days. These experiments included altogether 223 flies In general, the female outlived the male in the different lots Only in one lot fed with sugar solution did both male and female flies live to the end of 18 days

Swarm

Cameron (1922, p 16) described the various kinds of swarms, which consist of females, males and mixtures of both Enderlein (1921, p 198) mentioned a swarm of males as the only one seen during ten years' collecting Near the Biological Station small swarms of females are very common in the late afternoon, especially after a warm, clear day But swarms of males are seldom seen unless one looks particularly for them They form higher up in the air, at least about 10 feet from the ground Most flies captured from such a swarm are males, but from the behavior of the flies it appears to be a mating swarm The flies hover steadily for a while and then suddenly dart for short distances. On calm evenings such swarms often form in open exposed places, but when there is wind, they are found in more sheltered positions, such as small clearings among the woods One evening while collecting flies among the aspens near the Biological Station, the writer saw a small swarm of females over a sweater thrown on a stump, with many individuals searching and burrowing among the woollen fibers

Sex ratio

Collectors of Simulium very rarely capture male flies by the net, and the writer had the same experience in the Douglas Lake region The small number of males in the field led to a study of the sex ratio in the reared specimens The following figures show in every case an approach to the 1 1 ratio *S vittatum* Zett, 706 707, *S jenningsi* Mall, 135 145, and *S venustum* Say, 35 43

Oviposition

Place — Oviposition has been observed by different investigators and found to be of two types (1) below the surface of water, and (2) at the water-level Britten (1915, p 170) and Edwards (1920, p 237) described the oviposition of two British species at a depth of from a few inches to one foot under water, and Comstock (1925, p 823) observed that *S pictipes* Hagen deposited the eggs on the rocks by darting into the thin sheet of water and out again Records (Webster, 1887, p 458, Needham, 1901, p 408, Knab, 1916, p 281) of the process in other American species show that they all belong to the second type The observation of the writer on *S vittatum* agrees with those of Emery (1913, p 330) and Pomeroy (1916, p 8) on the same species, that is, eggs are deposited at or near the water-level Eggs of *S venustum* have been found on grass blades also near the surface of the water

The fly, in search for a suitable oviposition place, hovers over the water and alights on some object just above the water-level Generally it selects a place with a thin film of water, or where its front legs can rest on dry ground while the tip of the abdomen reaches the water's edge In Maple River the many long cat-tail leaves, bent down and floating in the stream, present a very favorable condition for egg-laying Although the body of the fly is normally above water, it remains undisturbed if the swaying of the leaf should carry it under water for a moment It is enveloped within an air bubble and often continues laying eggs Flies have been submerged by holding the leaf under water for 1–5 minutes Some of them stayed in the same position, others crawled about, and, letting go their hold, rose up to the surface within the air bubble, all were dry upon emergence from the water

Oviposition occurs also outside the running stream In the shallows of the protected Maple Cove eggs are often found on the stems and bent-down leaves of small emergent plants These may be quite near the shore-line or farther out in the lake up to a distance of 70–80 feet, and they are from 50 to 120 feet from the actual breeding place

Time — In northern Michigan oviposition occurs from about 4 o'clock P M to dusk, with the greatest activity from about 5 to 8 P M After a calm, warm day the flies are most active, and very numerous In Maple River, cat-tail leaves, bent down to floating position in water, are literally covered with egg-masses, several layers deep, after one evening's activity Sometimes the masses even extend beyond the edge of the leaf Occasionally fresh egg patches were found in the early morning, but no oviposition was observed, nor were newly laid eggs seen between 9 A M and 4 P M

Throughout the season, from the middle of June to the middle of August, eggs were found in Maple River, but the heavy oviposition lasted about four weeks In 1926 it was already heavy when the first record was taken on June 15, the numbers decreased after July 10 In 1927 the period of extensive laying began toward the end of June and lasted longer than during the previous season On days of great activity hundreds of flies were hovering close to the water and producing a low buzzing sound Often 4–6 flies were seen ovipositing at the same spot, a section of a cat-tail leaf one foot long might have as many as 50–60 flies depositing eggs at the same time Usually a fly does not deposit all the eggs at one place, but often crawls to some other spot or flies away and then alights again to continue the process Flies have been observed to continue egg-laying for 1–3½ minutes, most of them deposited the eggs in a string along the water edge

Number of eggs — Malloch (1914, p 8) pointed out that the large number of 5,000–10,000 eggs from one female recorded by Horvath was undoubtedly an exaggeration, being probably an estimate of eggs in one mass deposited by a number of flies Friederichs (1921, p 86) counted 500–1,000 eggs in the small egg patches that appeared to be deposited by one female Riley (1886, p 504) gave 500 as the number of eggs found in the ovaries of the American species In *S vittatum* the writer counted 306–320 well-developed eggs in the ovaries of reared specimens which had not oviposited

Mortality — Many females, dead or struggling to escape, were found stuck to the gelatinous matrix of the egg-mass On one occasion over 30 flies were counted on a section of a leaf about 1½ feet long Pomeroy (1916, p 9) observed a similar condition on the egg-mass on bridge piles

Many of these flies were removed and dissected for examination of the ovaries Some had finished egg-laying, others contained eggs varying in number, the highest being 250 in one fly This indicates that they became stuck by accident during oviposition The newly laid eggs are very sticky, but older eggs are no longer so, since the flies can crawl freely over the tan-colored ones and continue to deposit new layers of eggs without becoming trapped

In captivity — All attempts to induce oviposition in captivity failed Cages placed in the open under trees were provided with dishes of water containing aquatic plants and pebbles Thick sugar solutions or soaked raisins were supplied as food Both reared specimens (*S vittatum*) and those caught with the net (*S venustum*) were used When flies did not oviposit under such conditions, a cage was placed in the edge of the lake so that water in motion would be provided This is identical with the condition in Maple Cove, so far as water and objects for attachment are concerned, yet no oviposition occurred As concerns *S vittatum*, this failure was not due to a lack of proper food for the development of the ovaries, because the flies, when dissected, contained mature eggs Discussion of *S venustum* in this connection appears later

Oviposition was accidentally secured from two reared *S vittatum* flies One female was isolated after emergence in a 6-dram vial Water was supplied on a small piece of cheese cloth, but no food was given On the fifth day the fly died, but had laid eggs on the wet cloth These unfertilized eggs failed to hatch From dissection it was found that all the 152 eggs were from one ovary, the other was not well-developed and the eggs were less than half-sized In the other instance about 80 eggs were found on the moist wall of a half-pint jar in which both males and females had been kept No mating has ever been observed in captivity, and these eggs did not hatch, probably they also were unfertilized

Food

The food of Simulium flies, except the blood-sucking ones, is not definitely known In captivity, individuals of both sexes of *S venustum* and *S vittatum* take sugar solution readily and live very well on soaked raisins They also feed upon fresh honeysuckle leaves and take water from droplets on them Both species are recorded as blood-sucking, but *S vittatum* was not found biting, nor did it seem to be associated with *S venustum*, which is very annoying in the Douglas Lake region

The fact that both males and females can live 5–6 days without any food proves that food is not an absolute necessity, at least for that length of time after emergence The presence of fat-bodies in both sexes may serve to explain, at least in part, why they do not depend upon the taking in of nutritious material from the outside, even when they are active on the wing The fat-bodies in newly emerged females of *S vittatum* are very large, but as the eggs develop they gradually decrease in size Two flies kept on water alone oviposited in captivity This significant evidence indicates that the flies not only lived, but also completed the egg development and oviposition without taking any food Water is necessary, for if they are not supplied with it they die within 2 or 3 days Perhaps this supports the general supposition that the flies which do not suck blood live on plant juices

Blood sucking and development of ovary

The dependence of ovary development on a blood meal was studied by Pomeroy in *S venustum* Say (1916, pp 30–34) and confirmed by Cameron in *S simile* Mall (1922, pp 19–20) The writer also found that, without the engorgement of blood, the *S venustum* fly, either reared or captured, never contained ovaries with developed eggs, although eighteen of the flies dissected had lived for 9 days. But *S vittatum*, although known as a blood-sucking species, does not attack man in the Douglas Lake region, and so presents an interesting condition for study

As mentioned in the section on oviposition, two specimens of *S vittatum* deposited eggs in captivity without taking any food at all Other reared specimens kept on sugar solution or water alone have been dissected, ranging from those just emerged to those 5 days old Ovaries of newly emerged flies contained small round ova, corresponding to what Pomeroy called stage 2 After 1 day, the eggs were about one half the size of mature ones and some began to assume the oval shape After 2 days, they were about three fourths mature, although one of the eight flies dissected contained fully developed eggs, after 3 days, the eggs became mature and had the typical triangular shape They were very sticky, adhering to the needle and scalpel during dissection When the flies lived for more than 4–5 days the eggs showed no further growth From this study it is evident that in *S vittatum* the development of the ova is not dependent on a blood meal or any other food, and that the fat-bodies, probably present, supply the necessary material for growth (see section on food)

The presence of fat-bodies is, however, not an indication that the female does not need food for ovary development Both *S venustum* and *S jenningsi* Mall have them, though proportionately less than those in *S vittatum*, but when kept under the same conditions as *S vittatum* their ova *do not develop at all* This tends to show that the blood-sucking forms require a definite food in order to produce progeny, yet *S vittatum* appears to be an exception As mentioned at the beginning, *S vittatum* is not a pest to man in the Douglas Lake region But if it should be found to attack animals, it would prove to be a form that could complete its ovary development with or without a blood meal The condition of the alimentary tract of the flies captured while ovipositing gave no indication that they had taken blood Blacklock (1926 b, p 210) found small amounts of altered blood up to 4 days after breeding Therefore, if *S vittatum* does not suck blood at all in the Douglas Lake region, it must be a species which has different food habits in different localities It is definitely a biting species in Kansas, Hunter (1914, p 311) used it in the experiments on the attempted transmission of pellagra.

In this connection two other instances may be mentioned

S venustum, the well-known pest, is recorded by Needham (1901, p 408) as "peaceably disposed" in the Adirondacks, and by Sanderson (1910, p 27) as "*causing very little annoyance in the White Mountains*" *S hirtipes* Fries is the species accused by him of biting, Comstock (1925, p 824) also called it the scourge of the *fishermen in the mountains of the northeastern states* Near Ann Arbor *S hirtipes* occurs in the Huron River A few reared specimens were kept on sugar solution, and two flies, 4 and 5 days old, contained ovaries with well-developed eggs Although the number is too small to be significant, distinct differences from the ovaries in *S venustum* and *S jenningsi* were shown If this indicates a food habit different from these two species, then *S hirtipes* is not a blood-sucking form near Ann Arbor

Both Pomeroy and Cameron found the simultaneous occurrence of mature and immature eggs in the ovaries of certain *captured* adults, but they had no way of knowing the history of these individuals It may be of interest, therefore, to note that the ovaries of the two specimens of *S hirtipes* mentioned above contained ova of two sizes (1) about 30–50 mature ones, and (2) a large number of the small, round type Newly emerged females have been examined, their ovaries contained small ova of uniform size These two flies were fed with sugar solution One died after 4 days and the other had lived 5 days when dissected Both had *not* oviposited, so that here the condition is different from that which Pomeroy called "stage 5," that is, a few mature ova left from an earlier oviposition in the ovary with rudimentary eggs

The writer has found two cases corresponding to "stage 5" among individuals stuck to egg-masses The condition of these small ova does seem to indicate, as Pomeroy stated, that they may be developed later for another oviposition, but the writer has not obtained enough evidence to support such a supposition

Parasite

Two nematode parasites were found when preserved adults were dissected One *S hirtipes* Fries female contained a large worm 17 mm long, which filled the abdomen completely One *S jenningsi* Mall female had a small worm about 3 mm in length coiled around its ventriculus Both imagoes were reared from pupae collected from the Huron River, in which locality the *larvae* of these two species were found to be occasionally parasitized by nematodes

The writer is able to find only one record (Swinton, Edwards and Boylis, 1913, p 391) in the literature of a nematode in a Simulium adult Swinton found a specimen of *S ornatum* Mg on a window-pane, after killing it with a drop of benzine, he suddenly noticed a worm coming out of the abdomen of the mounted specimen In his paper on the parasites of Simulium larvae, Strickland (1911, p 326) concluded that Mermis "inhibits the development of the histoblasts to such an extent that pupation becomes impossible" The two worms found by the writer must have been carried over from the larval stage, because the reared flies were dropped into alcohol soon after emergence and had no time to become infested Strickland (p 311) pointed out that in the larvae parasitized with histoblasts of moderate size the worm may have entered the body cavity after the disks were somewhat developed This possibility may explain the presence of the small worm in *S jenningsi* It might thus have succeeded in pupating because of late infestation, but the large parasite in *S hirtipes* appears to be an exception to the observations of Strickland

PART II EXPERIMENTAL SECTION

GENERAL STATEMENT

It has long been known that the exclusive breeding place of Simulium is in swiftly running water, as is well attested by the numerous literature records on this point listed by Wilhelmi (1920, p 133) But after reviewing the literature one is surprised to find only the mere recognition of this fact and no study at all of the factors involved In spite of the fact that running water is claimed to be essential to the life of the larvae, not one measurement of the actual velocity of the current in the habitat was taken by these investigators The only record of which the writer is aware is that of Tonnoir (1925, p 216) in his study on Australian Simulium, namely, that the larvae are found ' only where the speed of the current is about one foot per second" Furthermore, with no other evidence than that the larvae usually died within a few hours in standing water, earlier investigators claimed that the oxygen requirement of these larvae is very high and can be satisfied only by the much-agitated water in a swift current

In order to make a thorough study of this requirement of the larvae for running water, experiments have been carried out to analyze the possible factors concerned and to ascertain the relative influence of each The experiments fall into three groups (1) on current rate, (2) on the food factor, and (3) on the oxygen supply All experiments in the natural habitats were performed in the Douglas Lake region Laboratory experiments were conducted both at Ann Arbor and at the University of Michigan Biological Station

EXPERIMENTS ON CURRENT VARIATION

Current rates in natural habitats

Before experiments were planned, a study was made of the current rates in the natural habitats in the Douglas Lake region The current was measured with a small glass tube bent at right angles and the results were calculated from the following formula $V = 0\ 977 \times \sqrt{2\,gh}$ V = velocity, in terms of feet per second, g = gravity, 32 16 feet per second, and h = height of water column in the upright arm of the tube, when the other arm is set in water against the current Correction was made in the value of h by subtracting from the actual reading the effect of capillarity

A careful study of the water velocity in situations where Simulium larvae occurred, except in the vertical falls, showed that the current rate varied from 0 56 to 2 75 feet per second, with the majority of the records occurring between 1 and 2 feet per second The current rate was even greater where the water drops over boulders or log dams in a perpendicular fall, but the glass tube was not usable in this position Although the highest possible rate in the natural habitat has thus not been specifically determined, the minimum rate, which was of greatest importance in this connection, was critically studied, especially in Bessey Creek

The upper channel of this stream consists of stretches of shallows with sandy bottom connecting deeper depressions at the concave or outer side of the numerous bends These connecting slopes are favorable locations for a series of measurements, since they represent a natural current rate gradient and support a population of Simulium larvae and pupae Three typical slopes were selected and four series of measurements were made The minimum rate, i e that below which no Simulium larvae occurred, was found to be 0 56 foot per second in two of the series, 0 79 foot per second in another, and 0 97 foot per second in the fourth In a small side channel, where a group of larvae were established on Potomogeton leaves, the current was also 0 56 foot per second This minimum rate as determined is for Bessey Creek only, where *S vittatum* and *S venustum* are the predominating species, it should not be taken as the minimum rate for all species and in all kinds of streams

Sediments -- In connection with the study of current, it was shown clearly that, when other factors were equal, the sediment on the supporting objects had a close relation to the presence or absence of the larvae on them For instance, in the third of the series referred to above, the minimum rate, instead of being 0 56 foot, was 0 79 foot per second, but there was no environmental difference between this and the first two series other than the presence of sediment on objects at points with lower rate Even at a point with a rate of 0 79 foot per second, larvae were present only on the under side of a leaf the upper surface of which was partially covered with sediment At a position with the *same* rate, in the fourth series, similar leaves had a rather thick layer of sediment on both sides and no larvae were found, under these circumstances the minimum rate was 0 97 foot per second The cause of sedimentation differences under the same velocity in the same stream is unknown, but it appears to be either or both of two things (1) the time through which sediment has been accumulating, or (2) the relative distance from the shallow swift section upstream

Transplantation

In studying the current variation it is necessary to secure such conditions that, while the current rate varies, the other factors remain unmodified Several streams in the Douglas Lake region presented such favorable conditions because within a short distance of places where larvae occur normally the velocity may become much lower while the food material and the chemical nature of the water remain unaltered This favored the transplantation work which was carried out in Maple River, Carp Creek and Bessey Creek

In Maple River

Maple River arises in the extreme end of Maple Cove Quiet lake water is thus gradually converted into unaltered running water The current becomes about 1 5 feet per second near a cat-tail patch about 20 feet downstream from the lake margin Here larvae suddenly appear in great numbers, mostly on long cat-tail leaves that are bent and floating in water, but also on Potamogeton and other plants From this point lakeward (upstream) the current decreases gradually until it disappears in the shallows of the cove This section with varying rates of current was selected for the transplantation experiments

Seven stakes were set in a row, with the first nearest to the cat-tail patch and the others successively upstream with the last farthest out in the lake Cat-tail leaves bearing larvae and pupae were cut off at the leaf base and gently dragged in water to the different stations and tied to the stakes, care being taken not to dislodge the larvae by jerking the leaves too much or lifting them out of water At the same time fresh cat-tail leaves were tied to each station to provide more objects for attachment The current rate at each station was measured In general, there was some decrease in the numbers after the transplantation, but if the majority remained they were recorded as established Records were taken every second day for 20 days and at longer intervals subsequently From observations extending over six weeks the following results were obtained

Station 1 – Current variation, 0 97–1 26 feet per second throughout period of observation Larvae well established and pupated normally Station observed for only 16 days, owing to disappearance of stake supporting transplanted leaves

Stations 2–3 — Stations located near beginning of river Station 3 three feet upstream from Station 2 and slightly within margin of lake Current variation 0 79–0 97 foot per second during whole period of observation Transplanted larvae well established and subsequently pupated Eggs hatched and resulting larvae thrived Later in the season, on fall of the lake level, the current rate was nearer 0 79 and larvae decreased in numbers, though some of various sizes present till end of observation period

Stations 4–5 — Out in lake, 2 feet apart, Station 4 about 10 feet from Station 3 Current 0 58 foot per second, sometimes slightly higher Transplanted larvae, mostly fifth and sixth instars, established at both stations and pupated Larvae hatching there disappeared after reaching fourth instar

Station 6–7 — Station 6 about 15 feet farther in lake from Station 5 and Station 7 about 5 feet beyond Station 6 Current 0 40 foot per second (lowest rate measurable by available apparatus), not detectable later in season Larvae disappeared from supporting leaves, very few remaining 2 or 4 days after transplantation Larvae, full-grown at transplantation, pupated and emerged successfully Eggs, deposited locally or transplanted, hatched, but resulting larvae disappeared within 2 or 3 days

Results — When larvae were transplanted from their normal habitats to localities with all conditions the same, except for reduction of the current velocity, they became established only where the current rate was 0 58 foot or more per second, the medium-sized larvae of the fourth instar appeared to require a current higher than 0 58 foot per second

In Carp Creek

Carp Creek is a swift stream fed by underground water and flows through a deep, wooded valley into Hurt Lake About half a mile from its mouth a beaver dam over 200 feet long and 3–5 feet high produced a waterfall of considerable volume near the steep east bank Simulium larvae, *S venustum* mixed with *S vittatum*, occurred in large numbers in the overflow, but were present in the creek in smaller numbers The beaver pond above the dam was very extensive, at its beginning, where the swift stream became gradually converted into the quiet water of the pool, there was found a natural graded series of current velocities *This favorable location was selected for transplantation work to* find out the minimum rate required

Convenient objects in the stream were chosen as the stations and the current rate at each was measured In the first series, four stations had the following rates per second Stations 1 and 2, 0 97 foot, Station 3, 1 49 feet, Station 4, 1 87 feet Sticks bearing a good supply of larvae were collected from below the beaver dam and were tied securely at the different stations When examined the next day, larvae were established at Stations 3 and 4, but had disappeared from Stations 1 and 2 Apparently the minimum rate was between 0 97 and 1 49 feet per second

A second series of four stations was then selected Sticks with a good supply of larvae were collected from below the beaver dam and carried over in a long shallow pan containing water This proved to be a good method The results from observations of one week were as follows

Station 5 — Current rate 0 97 foot per second After 2 days only 2 larvae out of about 20 were found on the stick, which was already fairly well covered with sediment, all had gone after 4 days

Station 6 — Current rate 0 97 foot per second After 2 days only 1 larva out of about 50 was left on the stick, which was covered with sediment After 4 days no larvae were seen

Station 7 — Current rate was 1 26 feet per second Larvae well established After 6 days most of the larvae shifted to the under side of the stick when the upper surface was covered with sediment

Station 8 — Current rate was 1 26 feet per second No larvae were present on the next examination, but the stick was much lower down than when it was fixed, indicating that it might have been interfered with in some way

Station 3 of Series 1. — Current rate was 1.49 feet per second. Larvae were established and still present on the seventh day after transplantation. Sediment was gradually accumulating; larvae shifted to the under side.

Results. — Larvae transplanted from a locality with a rate of 2.75 feet per second became established at a rate of 1.26 feet per second. Records of Stations 5 and 6 tend to indicate that they might establish themselves where the current rate was 0.97 foot per second, if the factor of sediment was eliminated.

In Bessey Creek

Only one series of three transplantations was made; no larvae were established at the new localities, but interesting observations were made on the behavior of the larvae immediately after the transfer from their normal current rate to a weaker one. In transplantation the plant leaf supporting a colony of larvae was cut off and gently dragged in water to the selected spot. Very few larvae were lost through this handling. But soon after the leaf was fastened the larvae became restless, they changed their point of attachment and turned their heads in different directions, as if testing the movement of the water. Very often they shifted to the under side of the leaf, or along the lower edge if the blade was in a vertical position, and were established temporarily. Some larvae actually loosened themselves from attachment and, as they spun the silk thread, were carried slowly downstream. They were able to stop spinning and remain suspended for a while to investigate their environment. Some began climbing back on the silk thread, but very few reached the original position. If the thread became attached to some neighboring object, the larvae crawled upon it. Most of them would start spinning again and were soon carried away downstream. On one occasion approximately one half of the original population were lost from the leaf within 20 minutes. This was a transfer from a habitat with a rate of 1.87 feet per second to a place where the current was 0.56 foot per second. In one transfer from a current rate of 1.26 feet per second to one of 0.40 foot per second the behavior of the larvae was the same, within 15 minutes most of the large and medium ones had disappeared from the upper surface of the leaf

DISCUSSION

From the results obtained from transplantation work, there are several points of interest to be considered

(1) When larvae are transferred to a current weaker than that of their normal habitat, some of them let go their hold within a very short time, as if in search of a more favorable environment Obviously, this behavior is not due to the food relation, because they could not have suffered, within a few minutes, from any decrease in the amount of food carried to them by the slower current The important factor of oxygen supply does have immediate effects upon organisms and it seems to explain the response of the larvae on the supposition that the weaker current cannot meet their high oxygen requirement But when the situation is examined closely, such an explanation cannot be applied The dissolved oxygen content of the surface water is high, and, furthermore, the water in contact with the body surface and anal gills is changed even with very slow current Under such conditions it seems difficult to suppose that the larvae are unable to effect adequate exchange of gases The very fact that not all the larvae left the new environment simultaneously is a proof that the cause of their restlessness is not suffocation It will be remembered that in the study on the current rates in the natural habitat in Bessey Creek a small number of larvae were found living normally in a current of 0 56 foot per second It is evident from these considerations that the immediate desertion of the new locality is not a vital necessity This behavior appears, therefore, to be a *mere response to the change of pressure It is obvious that,* with the slower current, the pressure of the running water against the body surface is diminished and that this difference is the first thing the larvae experience in the new environment It seems reasonable to suppose that, after finding themselves out of their normal surroundings, they would become restless It may be, therefore, merely a response to the immediate stimulus without involving relation to the other factors

(2) A small number of larvae remained at stations in very weak currents for a few days, but finally disappeared This was observed in transplantation in both Maple River and Carp Creek Although they did not become established, the very fact that they lived for 3 or 4 days where the the current rate was only one third of that of their normal habitat was significant, and showed that they secured oxygen from the slow-moving water On the other hand, the final disappearance of the larvae indicated that there were factors other than oxygen supply involved in their requirement for swift-running streams In Carp Creek, it appeared to be a matter of sedimentation, for the larvae disappeared when their supporting object was covered with sediment In Maple River, there was no apparent cause for their disappearance, but there was the problem of insufficient food If only one third of the normal volume of water passed through their fans in a unit of time, the amount of food they were able to strain was reduced accordingly It seemed, therefore, more plausible that the food factor, rather than the dissolved oxygen, would require 3 or 4 days to become effective

(3) The minimum current rate at which the transplanted larvae became established was found to be 0 58 foot per second in Maple River and 1 26 feet per second in Carp Creek It is very significant that the minimum rates differed so much in the two streams, one being a little over twice the other The disparity might be due to either a difference in species or a difference in the nature of the stream

The material used in Maple River was practically a pure *S vittatum* Zett population, that in Carp Creek, a mixture of *S vittatum* Zett and *S venustum* Say These two were the most common species in the Douglas Lake region and occurred together very often in both swift and moderate currents They were also found together in other parts of Maple River It is evident, therefore, that, although the larvae were not identical in the two transplantations, this difference in the current requirement was not one of species

Now, if the two streams are compared, they are very different in their source of water supply Maple River is formed exclusively from surface lake water, while Carp Creek is fed wholly by underground water The former has a temperature of 19° to 26° C during the summer months, the latter, from 10° to 14° C Considering the temperature factor alone, it would seem that the larvae in Maple River, because of a higher rate of metabolism, would require a swifter current than those in Carp Creek to get adequate oxygen and food supply Yet the result of the experiments was just the opposite, so that other factors should be examined Both streams have high content of dissolved oxygen, Maple River being about 62 per cent of saturation and Carp Creek about 60 per cent This shows that it was not because of lower oxygen supply that the larvae in Carp Creek required twice as strong a current as those in Maple River The other possible factor to be discussed is the food material in the streams Maple River has a typical lake plankton population, while Carp Creek, originating as it does from springs, has little chance to develop a plankton Quantitative plankton examinations revealed this fact If the amount of food that can be strained from a unit volume of water is much less in Carp Creek than in Maple River, it is evident that the larvae in the former need a much larger volume of water to pass through their fans in order to obtain the same amount of food It seems possible, therefore, to conclude that striking lack of agreement in the minimum rates for the establishment of transplanted larvae is due to the difference in the amount of food material available in the two streams

Trough experiments in Carp Creek

In the transplantation work two possible imperfections had appeared (1) the current rate at the different stations, though in general quite uniform, was not perfectly so, and (2) transfer of larvae from their normal habitat to a different one might be too sudden for them to adapt themselves, especially when the new locality had a much weaker current It seemed advisable, therefore, to contrive an arrangement in which the current rate could be regulated and the velocity be decreased gradually, all other factors remaining unmodified

Equipment — The overflow from one end of the beaver dam came down to a shelf and forward over a natural slope into the creek. This slope, with its abrupt drop of approximately one foot, was utilized for the trough experiments. A water reservoir was built near the edge of the shelf and water was admitted into a parallel series of four long troughs through four openings in the headpiece, which was set firmly at the edge of the slope. Each opening, which was 2½ inches in diameter, was fitted with a movable metal shutter by means of which the amount of water coming through could be regulated. The reservoir above the headpiece provided a steady stream into the troughs, even though the volume of water from the beaver dam might vary from time to time. A side channel served as an outlet or overflow when the water-level in the reservoir came to within 2–3 inches of the top of the headpiece. Each trough was 12 feet long and had a maximum depth of 4 inches. One end rested on a support built on the headpiece just below the opening. The other end was adjustable to various heights, being suspended by wire to a crossbar. With the angle of slope adjustable and the volume of water regulated by the shutters, it was possible to obtain various current rates in the different troughs. Here, then, though all other factors remained the same as in the normal habitat, study was made of one single factor, namely, that of current variation.

Sticks bearing a good supply of larvae were collected from Carp Creek in the immediate vicinity of the troughs and gently introduced into them. They were held in place in the trough with wire. Examinations were made every second day, the current rate was measured and the number of larvae recorded. In most cases an actual count was made. These troughs were set up on June 29, 1927, and were kept under observation until August 16.

RESULTS

Trough 1.—Larvae introduced on June 29 were kept under observation until August 16. They were attached to a stick approximately 4 feet long and slightly more than an inch in diameter. It was comparatively straight, but had two short bends which produced local current accelerations by being too close to one side of the trough. Other local ripples were produced at the lower end of the stick where there was a drop in the water-level, especially when the amount of water in the trough was cut down. These three points, therefore, always registered higher current rates than along the straight, smooth sections of the stick. This made possible the observation of the larvae at points with small differences in the velocity rates. For the first three days the velocity was about 3.5 feet per second and the larvae were well established. When the velocity was gradually reduced, the results were as follows: (1) *During reduction of rate to 1.2 feet* per second, the larvae were not affected and did not shift around, (2) When the velocity was cut down to 1.1 feet per second, a few large larvae migrated, but most of them remained, (3) With a rate of 0.9 foot per second, larvae disappeared from some points and remained at others — in general, few *large* larvae stayed in this velocity and then never more than 2 or 3 days, but *medium* and *small* ones persisted at this rate, (4) For small larvae, the rate of 0.8 foot per second appeared to be the critical point, because only twice were a few individuals found in such a slow current, (5) At points with rates lower than 0.8 foot per second, larvae never remained.

Trough 2. — This trough was used for a study of maximum rate. One stick bearing larvae was placed in the trough on June 29 and kept under observation until August 16. The initial current rate was 3.5 feet per second on the first day, but after a gradual increase reached 6 feet per second on the eighth and was maintained thus throughout the rest of the period. This was the highest velocity in this trough set-up. The first count made on the fifth day showed 28 larvae. This number *gradually and slowly* decreased, but there were *new pupae* appearing throughout the whole period. After 43 days there were 3 larvae and 4 pupae on the stick. This record shows that the larvae lived in a current of 6 feet per second for a long period. This rate, however, was not high enough to dislodge them from their attachment. It would have been interesting to determine the exact maximum rate, but this experiment was not extended further because the *minimum rate* was, after all, the critical matter in this work.

Trough 3. — This trough was operated to determine the minimum rate The results agreed with those from Trough 1 The only additional finding was the record of a mixed group of medium and small larvae established at a point where the rate was 0 8 foot per second

Trough 4 — For the first 10 days this trough was operated with a current rate of 3 5 feet per second and larvae were well established It was then changed into a study on slow current In general, the results were like those from Trough 1

A similar arrangement of troughs had been set up below the beaver dam in the previous summer (1926), but observations were made over shorter periods and the results were not then considered conclusive However, when these are compared with the results of 1927, it is significant to find that the minimum rates determined are the same

Larvae in standing water

It is repeatedly stated in the literature that larvae can live only a few hours in standing water, the longest period recorded is 48 hours (Pomeroy, 1926, p 19) in shallow water barely covering them The writer has kept them for much longer periods The results of these experiments are to be presented and discussed in the section on oxygen supply, but the fact that many larvae have been maintained for 8–14 days and a few for 23 days in standing water should be recorded here It definitely shows that larvae can live for several days in shallow water *without* any current at all

EXPERIMENTS ON THE FOOD FACTOR

Filtration of lake water

Equipment — In order to remove the food material from the water without otherwise changing it, a sand filter was devised Since the natural medium for *S vittatum* at the origin of Maple River is formed from surface lake water, the same kind of water was used in the experiment Current was provided by leading the filtered water into a trough, on the walls of which the larvae were induced to attach themselves

The filter tank was of galvanized iron, 14 inches in diameter and 28 inches deep Two drainage openings at the bottom were fitted with stopcocks to regulate the flow The gravel foundation consisted of several layers of different sizes, which were as follows, beginning at the bottom (1) gravels, 1-3 inches in diameter and about 4 inches deep, (2) gravels, ½-1 inch in diameter and about 2 inches deep, and (3) smaller gravels about 2 inches deep Superimposed was the sand layer, about 12 inches deep Tyler graded screens were used to sift the sand, in order to get grains of different sizes in the proper proportions for a filter bed The sand was taken from the clean, exposed beach and thoroughly washed before it was put into the filter tank Water was let into the filter at the top from the big water reservoir in the aquarium building This reservoir was kept filled with fresh, unmodified lake water by a power pump A wooden trough, 54 inches long, received a steady stream from the bottom drainage outlet of the filter tank A similar trough was set up as the control, receiving water directly from the main reservoir

S vittatum larvae were collected from Maple River on July 18, 1927 A steady stream was first started in each trough, after which larvae were introduced one by one with a pair of forceps With the larva held loosely between the curved points, the forceps were placed in water against the side of the trough If the larva was in such a position as to be able to reach the board with its mouth-parts, it clung there and drew its posterior end down against the side to effect attachment If the larva was washed away from between the prongs, it usually spun a silk thread as it was carried downstream, one end of which remained anchored to the forceps By gently pressing the forceps against the side of the trough, the silk strand would usually adhere to it, thus bringing the larva also nearer the side to which it might attach itself, either directly or by climbing back on the silk thread until it reached the board Of course, some larvae were carried away by the stream, particularly if when put into water they did not produce any viscous material on the forceps and therefore could not begin spinning the silk thread By careful manipulation larvae were introduced without much loss In order to secure in the two troughs material strictly comparable as regards ages, care was taken to introduce a few of the same size into the experimental trough, and then the same number of similar size into the control By repeating this alternate selection process many times, ultimately both troughs were provided with larvae of medium sizes, the proportions of each size thus being as nearly the same as possible in the two troughs By regulating the amount of water supply and the angle of inclination, these two troughs were kept with approximately the same current rate, 1 4 feet per second, throughout the period of observation Examination was made twice a day and the number of larvae present, of pupae transformed, of emergences and deaths was recorded

In order to test the efficiency of filtration by this filter bed, water from the drainage outlet at the bottom was passed through a plankton net, but no plankton organisms were recovered It was then passed through a fine filter paper, but nothing was collected after 10 or 15 minutes' filtration It was only after longer periods that a few extremely minute algae might be seen on the paper under the microscope This study shows that the possible food supply was almost wholly removed by this filtration When the feeding method of the larvae is considered, the small number of minute algae present became really negligible as food From the eighth day, the drainage gradually became slower, on the next morning, about one-half inch of surface sand was scraped off The removal of this coating showed the clean sand underneath and normal filtration was restored Fresh, clean, graded sand was added to maintain the depth of the sand layer Only one more scraping was needed to keep it working until the end of the experiment

Results — The results from this set of troughs are summarized in Table I No marked effect was produced on the larvae by keeping them in filtered water It should be noted that the filtration did not remove every possible food material contained in the water, it merely removed the plankton organisms that normally constitute the food for the larvae Whether the larvae were able to secure nutrition in the filtered water in some form other than plankton was not determined It is evident that with a greatly reduced food supply, the larvae still lived to pupation, although it was somewhat delayed While the last larva in the experimental trough pupated only 5 days later than that in the control, marked differences were found earlier in the experiment As shown in the table, 43 per cent of the pupation in the control trough occurred within the first 4 days and 50 5 per cent within the next 4 days, making a total of 93 5 per cent, but in the experimental trough only 39 2 and 24 per cent occurred in the same periods, respectively

With reduced food, growth should be affected and the mature larvae in the experimental trough should be proportionately smaller than those in the control Since actual measurements of the larvae could not be taken without removing them from the

TABLE I

Effects of Filtered Lake Water on Larvae and Pupae

	Experimental trough Filtered lake water	Control trough Unmodified lake water
Duration of experiment	32 days[*]	26 days
Larvae introduced	212 '	220
Larvae dead	23 "	19 '
Larvae lost	59[†] "	15 "
Larvae pupated	130 '	186 '

Duration of Pupation	Number	Percentage	Number	Percentage
Within first 4 days	51	39 2	80	43 0
From 5th to 8th day inclusive	32	24 6	94	50 5
From 9th to 12th day inclusive	39	30 0	10	5 3
From 12th to 16th day inclusive	7	5 3	1	0 5
On 21st day			1	0 5
On 26th day	1	0 7		
Total	130	99 8	186	99 8

[*] The last pupa had not emerged when the experiment was discontinued

[†] The large number of losses was due to external disturbances, the trough was without a stream for a short period, once on the third morning and another time on the thirteenth day Except for these losses, the number of larvae disappearing from the trough was comparable with those in the control trough

trough, such a study was not made, but all the pupal cases in each trough were preserved after the emergence of the adults Owing to the membranous folds of the abdomen, the pupal skin could not be accurately measured The cocoon, however, was of firm texture and provided a good index of the size of the larva *S vittatum*, *S venustum* and *S jenningsi* all have cocoons of the wall-pocket type, with cases of distinctly different sizes corresponding to the size of the larvae of each species Furthermore, as pointed out in the description of cocoon-spinning, the dimensions of the cocoon were mainly determined by the length of the larva, because it was attached at its posterior end throughout the *whole* process Therefore the cocoons from these two troughs were measured to get the relative size of the pupating larvae Measurement was taken from the apex of the cocoon to the middle of the rim at the open end No attempt was made to get the length between the apex and the two corners in front, because they were not well defined and parts might be broken off when removed from the trough If the apex of any cocoon was not complete, it was discarded and no measurement taken Altogether, 167 cocoons from the control trough and 104 from the experimental trough were measured Table II gives the measurements The cocoons from the experimental trough were grouped into two sets (1) those resulting from pupae which transformed within the first 4 days, and (2) those belonging to pupae that transformed after the 4th day Cocoons from the control trough were also measured in separate lots, but they were put together because there was no difference in size between the early and the later cocoons The average length is 3 62 mm for cocoons from the control trough and 3 08 mm for those from the experimental trough When plotted, each curve has a mode at a different point cocoons from the control trough had the highest figure, 3 42 mm, those from pupae of the first 4 days in the experimental trough the next lower, 3 15 mm, and those after the 4th day the lowest, 2 88 mm These figures clearly show the smaller size of larvae in the experimental trough, apparently because of the effect of the much reduced food supply This experiment shows that larvae of the *medium to mature stages* continued to develop and transform to adults when the food supply, i e the plankton in the water, was almost, if not completely, removed

Larvae in well water

Standing water cultures — In some standing-water cultures, aërated well water was used This was underground water that had passed through deep layers of sand and was obtained by means of a hand pump and a long iron pipe driven deep into the ground Microscopic examinations had shown the water to be free of organisms In starting a culture, although small amounts of lake water and possibly some organisms were introduced adhering to the larvae, the amount of food material that might be present in such a culture was extremely limited But larvae lived 16 days

TABLE II

MEASUREMENTS OF COCOONS FROM THE EXPERIMENTAL TROUGH WITH FILTERED WATER AND FROM THE CONTROL TROUGH

Length of cocoon in mm	Control trough number of cocoons	Experimental trough number of cocoons	
		Pupated within first 4 days	Pupated after 4th day
2 34		1	
2 47		1	2
2 61			4
2 74	3	2	14
2 88	12	8	18
3 01	15	6	9
3 15	26	9	8
3 28	24	7	
3 42	28	6	1
3 55	27	2	2
3 69	14	2	1
3 82	14	1	
3 96	2		
4 09	1		
4 23			
4 36			
4 50	1		
Totals	167	45	59

in one culture, in another, 19 larvae (18 8 per cent of the original population) of various sizes were still alive after having been in well water for 10 days In these cultures the last pupation was recorded on the 7th or 8th day, and no growth was apparent in the younger larvae

Well-water trough — An attempt was made to study the larvae when kept in a stream of aërated well water Two carboys were used as the reservoir, a siphon was arranged to lead a small, steady stream into a 2-foot trough, on the wooden board of which the larvae were induced to attach themselves Few were lost from the trough while the stream was running Under these conditions larvae lived as long as 8–9 days Since only fresh, pure well water surrounded the larvae, this record can be taken as representing complete starvation

Larvae in damp chamber

Frequently larvae were left in collecting jars after the contents were poured out If the jars were stopped tightly and the larvae remained wet some were found alive after 3 or 4 days, sometimes they lived for 7 days Such larvae had no chance to take food

EXPERIMENTS ON OXYGEN SUPPLY

Standing-water cultures in open vessels

Cultures — Previous investigators have claimed that the larvae die within a short time in standing water They have explained this phenomenon as due to insufficient oxygen supply, but no experiments were performed to support or disprove this supposition Attempts were made, therefore, to keep larvae in standing water and to study the conditions critically

Six different sets of experiments were made, all essentially of the same general character In the first five, 692 larvae of *S vittatum* were used, in the sixth, about 400 larvae of *S vittatum* and *S venustum* mixed All cultures were kept in the aquarium building, where temperature conditions approximated closely those of the habitats from which the experimental larvae were secured

Details of experiments cannot be presented here, they are on file in the office of the Graduate School and in the Department of Zoölogy, University of Michigan

The results show that some of the larvae can live in quiet shallow water for several days The longest period observed was 23 days for a few small larvae and 14 days for large ones Even with shorter periods of 6–10 days, during which the majority gradually died, the period was too long to account for the death of the larvae simply on the basis of a lack of adequate oxygen supply in the medium In a critical examination of the conditions, the following data should be considered

(1) *The dissolved oxygen content of shallow water in the open vessels* Since the quantity of water in these cultures was not sufficient to make a gas analysis, a study was made of the rate of absorption of oxygen by water with very low oxygen content It was found that in water 2½ inches deep, the oxygen content reached 25 per cent of saturation in 1 hour and 33 per cent in 3 hours In water 1 inch deep, the oxygen content reached 56 per cent of saturation in 3½ hours and 60 per cent in 4½ hours After this concentration was reached, it stayed around 60–65 per cent in water ½–1½ inches deep, whether the water had stood for one day or several days This percentage was about the same as that in Maple River and Carp Creek It is evident, therefore, that the actual amount of dissolved oxygen in the standing-water cultures was not lower than that in the natural habitat and, so far as oxygen content is concerned, ought to be sufficient to meet the requirements of the larvae

(2) *Temperature and the resistance of larvae in standing water* — It was observed that collections made on warm days usually had a higher percentage of deaths than those made on cooler days Furthermore, material from a cold stream, such as Carp Creek, suffered much more in the transportation from the field to the laboratory than did the material from warmer waters The experiments showed that larvae can endure cold, *standing* water much better than standing water whose temperature is higher than their natural habitat

(3) *Overcrowding* — Overcrowding of larvae in the limited

space may be one of the reasons why the majority usually died off within the first day After the removal of the dead subsequent to this initial loss, the majority of the survivors lived in these cultures for 3-4 days, a few individuals existed for 6 14 days In the field, the author commonly selected sticks or plant leaves with a large population of larvae and then subjected them to the conditions of a small collecting jar On being brought to the laboratory, the larvae were seldom divided into different vessels Since the thick colonies in the natural habitat had fresh water flowing over them, they met a different condition when so crowded and in water not moving But with reduced numbers they fared much better in the same vessel

Standing water with known oxygen content

Method — In order to study the larvae in water with constant dissolved oxygen content, particularly with small amounts of O_2, a series of experiments was performed Two 250-c c bottles were filled with the same kind of water according to the usual procedure of collecting samples for gas analysis Into one of them were introduced 5 larvae, after which it was stoppered tightly, the other was used for the dissolved oxygen analysis In this series of experiments Ann Arbor city water was used Preliminary experiments had shown that larvae lived well in this water if aerated It is underground water obtained from artesian wells, analysis had shown it to be practically devoid of dissolved oxygen When water with very low oxygen content was desired, the tap water was drawn with a rubber tubing inserted into the faucet with the outlet end of the tube kept under the surface of water in a large circular aquarium which was used as the common supply for the two bottles in each set of experiments To obtain water with a little higher oxygen content, the tap water was allowed to fall gently without agitation on the wall of the aquarium, after various periods of standing, the bottles were filled For experiments with high oxygen content the water in the aquarium was aerated with compressed air before it was siphoned into the bottles

A sample for dissolved oxygen analysis was taken at the time when the bottle was filled and another one at the end of the experiment from the water in the bottle Temperature varied from 14 4° C to 22 2° C

The material used in these experiments, *S jenningsi* Mall mixed with some *S venustum*, was collected in the Huron River

Results — Details of the experiments will be omitted The results may be summed up as follows (1) When the water had a dissolved oxygen content of 15-23 per cent saturation, larvae lived from a few minutes to 13 hours, (2) When the dissolved oxygen content was lower than 15 per cent of saturation, larvae succumbed within a few minutes, (3) In water with a dissolved oxygen content of 72 80 per cent of saturation, the larvae lived 60-114 hours

Current and low dissolved oxygen content

After it was found that larvae could survive for several hours in standing water with a dissolved oxygen content as low as 15 per cent of saturation, an attempt was made to determine the results when the larvae were supplied with a current, the dissolved oxygen content of the water remaining low This required an arrangement by which the water had a steady current, but was not exposed to the air The two kinds of equipment which were used will be described separately

The Stirrer

Equipment — A cylindrical aquarium of 10-inch diameter was fitted with an axle which could be revolved freely when its upper end was attached to a motor Near the lower end of the axle was fixed a transverse bar bearing a metal blade, 2½ inches by 2½ inches, on each end When the axle was revolved, the blades pushed the water in front of them and thus created a steady current flowing over the wall of the aquarium This axle was so fitted that it could be easily removed or set up again

First, the larvae were put into the aquarium, in about 4 inches of water This was to prevent them from becoming established on the aquarium wall higher than the level of the upper edge of the metal blades In order to get them attached on the aquarium wall, use was made of the compressed air In the stirrer aquarium, when two or three rubber tubings were so arranged as to let the air bubbles come up along the wall, the larvae soon became established near the outlets When enough were attached for the experiment, all the rest were removed and the axle was set in place In order to reduce the high oxygen content resulting from the aération with the compressed air, more tap water was quietly siphoned into the aquarium beneath the water surface Then a thick layer of paraffin oil was poured over the surface of the water to protect it from the atmosphere When connected with a motor and set revolving, the stirrer produced and maintained a steady current flowing over the larvae A similar stirrer was set up as the control, but without the oil layer In this work the motor was mounted on a power table equipped with a series of pulleys so arranged as to provide a wide variety of different rates of revolution The axles of the two stirrers were separately coupled up by belts with pulleys giving the same speeds With the rate of 50 revolutions per minute, the current rate was calculated to be 2 feet per second

It was soon discovered that the layer of paraffin oil failed to prevent absorption of atmospheric oxygen by the water underneath it, although the rate of absorption was *distinctly retarded* This agrees with the unpublished work of Professor Paul S Welch on the efficiency of the oil layer as a means of *preventing* oxygen absorption While this manuscript was being prepared, Hill (1928, p 374) reported on the relative efficiency of different liquids for the exclusion of oxygen, likewise confirming the fact mentioned above According to Harvey (1928, p 63), Roberts has conducted, with similar general results, experiments "upon the rate of entry of oxygen into sea water covered with a thin film of oil" Therefore, in order to maintain a reduced dissolved oxygen content, part of the water in the stirrer was siphoned from under the oil and water fresh from the tap was similarly siphoned in to restore the original volume, this was repeated as frequently as conditions demanded Care was taken not to disturb the larvae or to lower the water-level This exchange of water was performed without stopping the rotation and few larvae were dislodged By this partial change of water the dissolved oxygen content was kept lower than that in the control-stirrer, although it could not be kept constant.

Results. — Table III gives the records of Stirrer Experiment I, in which the dissolved oxygen content was not reduced by the change of water. When the amount in the stirrer approached that in the control, the experiment was discontinued. Both experiment and control showed a certain gradual loss in larvae, but it was very similar in both. Also, since in both experiment and control the oxygen content was relatively high throughout the test, the loss in larvae indicated what might be expected in Stirrer Experiment II, apart from any possible additional effect of reduced oxygen. Table IV gives the records of Stirrer Experiment II. In general, the number of larvae lost from the wall was slightly greater in the experimental stirrer than in the control, but there was not any greater loss at the time of reduced oxygen content than during other intervals. In fact, after the oxygen content was at 1.50 c.c. per liter, the larvae did not become restless and very few were lost from the wall during the five hours when the

TABLE III

STIRRER EXPERIMENT 1

Date	Number of larvae and pupae				Temperature		Dissolved oxygen (c.c. per liter)	
	Experiment		Control		Experiment	Control	Experiment	Control
	Larvae	Pupae	Larvae	Pupae				
May 27								
2 P.M.	43	8	64	3	21.2° C	20.2° C	3.63	4.60
May 28								
9 A.M.	37	10	61	4	23° C	20° C	4.88	5.73
5 P.M.	34	10	60	4				
May 29								
9 A.M.	30	10	57	6	21.5° C	20.4° C	5.79	6.42
4 P.M.	28	10	53	6				
May 30								
10 A.M.	22	10	51	6	21° C	20° C	6.14	6.49
7 P.M.	18	10	42	6				

oxygen content was between 1.56 and 2.91 c.c. per liter. The losses in both experiment and control are very similar to those occurring in Stirrer Experiment I, in which reduced oxygen was not involved. Evidently reduced oxygen had no significant effect.

The Rotation Dish

The stirrer experiments showed that larvae were well established in the current when the dissolved oxygen in the water was varying between 1.56 and 3.70 c.c. per liter at 22° C., that is, from 17 to 41 per cent of saturation. In order to find the minimum limit of the oxygen content for the larvae, the rotation dish experiments were devised. Since the experiments on standing water with low oxygen content showed that some larvae were able to

TABLE IV

STIRRER EXPERIMENT 2

Date	Number of larvae and pupae				Temperature		Dissolved oxygen (c.c. per liter)	
	Experiment		Control		Experiment	Control	Experiment	Control
	Larvae	Pupae	Larvae	Pupae				
June 1								
2 P.M.	220		268		21° C.	19.8° C.	3.02	4.41
8 P.M.	205	5	253	6				
June 2								
10 A.M.	194	12	237	14	21.4° C.	19.3° C.	4.26	5.68
3 P.M.	184	15	230	20				
3.10 P.M.*								
5 P.M.	172	18	228	22	21.7° C.		2.91	
June 3								
10 A.M.	150	22	218	30	22° C.	20.2° C.	3.69	6.34
3 P.M.*								
5 P.M.	144	24			22.2° C.		1.56	
10 P.M.	141	21	210	32	23° C.		2.45	
June 4								
9 A.M.	132	26	190	39	23° C.	22° C.	3.55	6.43

* Partial change of water to reduce the dissolved oxygen content.

live as long as 13 hours in water with dissolved oxygen of 15–23 per cent of saturation, it was decided to study the effects of lower oxygen content not only in a current, but also in standing water In this way the relation between the actual amount of dissolved oxygen and the current might be discovered

Equipment — In order to maintain low oxygen content and at the same time a current in the water, tightly sealed vessels were rotated on a platform, which was then connected to a motor Tap water, known to be almost devoid of dissolved oxygen, was drawn into a large aquarium by letting the water flow gently against the wall with as little agitation as possible If a very low oxygen content was desired, water was drawn with a rubber tubing inserted into the tap faucet and the outlet end of the tube kept under the water surface of the receptacle Water was then siphoned from the aquarium into a bacteria dish 7 inches in diameter After it had overflowed the dish 1½–2 times its capacity, a sample for oxygen analysis was taken while the siphon from the aquarium kept the dish filled Then 5 larvae were placed in the dish and induced to attach themselves near or on its wall A heavy glass plate cover was slipped on so as to include no air bubbles and was sealed tightly with vaseline This dish was then set on the rotating platform A control dish was set up with the same water, with exactly the same method, and placed on a table (not rotated) At the end of each experiment, a sample for oxygen analysis was again taken from the water in the dishes.

After the experiment was started, the larvae were examined about every 10 minutes But in the beginning, or when the larvae appeared to be in a critical condition, an examination was made every 5 minutes In those experiments which ran over several hours, examinations were made every 20–30 minutes toward the end of the period When the control dish was examined, the larvae were continuously watched, usually for periods of 1 2 minutes and sometimes even 3–5 minutes If they showed no movement, the dish was jarred to stimulate them When they failed to respond to repeated stimuli a "no response" record was made In the experimental dish the rotation had to be stopped in order to make an accurate observation Usually the larvae showed movement upon the stopping of rotation or when the water came to a standstill after 1–2 minutes Most frequently, they moved in a characteristic way as if testing the current around them, or they might bend sidewise or wave the anterior part of the body If the larvae failed to move after 2 minutes, then the rotation platform was pounded in order to jar the dish, and their response or failure to respond was recorded Concerning the movement of water in the rotation dish, it should be mentioned that the current flowing over the larvae was not continuously of uniform rate When rotation first started, there was considerable lag of the water as compared with the speed of dish rotation, hence greater current, but it slowly decreased until the motion of the water acquired its nearest approach to the rate of rotation of the dish, after which the slow current thus produced against the walls of the dish was uniform In this set of experiments the important factor for this study was *not the actual current rate*, but rather the difference in the effects on the larvae of standing water as contrasted with moving water With the water moving, even though slowly, the medium in the immediate surroundings of the larvae is being changed all the time, and this constitutes the significant difference from the condition in the control dish where the water was standing still Furthermore, with each examination of the experimental dish, the rotation was stopped and started again, so that this increased the rate of water movement for short intervals

Results — The results from this series of experiments are presented in Table V The most significant point is that the larvae in every rotation dish resisted the low oxygen content better than did larvae in the corresponding control, no matter what percentage of saturation each set presented In fact, the dissolved oxygen in every control dish, except two, was slightly higher than that in the rotation dish, because the former was always set up after the latter and consequently the water in the supply aquarium absorbed more oxygen during this interval Since the two dishes of each experiment were set up under identical conditions, except that one had the water moving and the other quiet, the difference in results can be attributed only to the factor of current When

TABLE V

ROTATION DISH EXPERIMENTS

Experiment		Temperature		Dissolved oxygen (c c per liter)		Percentage of saturation		Duration of experiments	Results
No	Form	Beginning	End	Beginning	End	Beginning	End		
IV	Rotation dish	15.8 C	17.7 C	0.25	0.35*	2.5	24	3 hrs	2 no response 2 no response after 15 min. 1 no response after 30 min
	Control	16 C	18 C	0.34	0.76	3.4	7.6	3 hrs	5 no response
III	Rotation dish	15 C	18 C	0.34	0.59	3.3	6.1	1 hr 45 min	2 no response 1 no response after 25 min 1 no response after 35 min. 1 no response after 70 min.
	Control	15 C	17.8 C	0.59	0.85	5.8	8.8	1 hr	5 no response
VI	Rotation dish	16 C	18° C	0.76	0.97	7.6	10.1	2 hrs 20 min	2 no response after 30 min 1 no response after 38 min. 1 no response after 60 min 1 responded till end of experiment
	Control	16 C	17.8 C	0.85	0.97	8.5	10.1	2 hrs 30 min.	2 no response 1 no response after 15 min. 1 no response after 20 min. 1 no response after 30 min.

I	Rotation dish	14.5 C	19 5 C	0 78	2 98*	7 6	32	4 hrs	1 no response after 55 min 4 responded after 2½ hrs before glass cover shifted
	Control	14 5 C		0 78		7 6		38 min.	3 no response 2 no response after 15 min
X	Rotation dish	16 1 C	18 4 C	1 26	1.36	13	14	2 hrs 30 min	2 no response after 2 hrs 15 min 3 responded till end of experiment
	Control	16 1 C	16 C	1.36	1 53	14	16	2 hrs.	2 no response 1 no response after 12 min. 1 no response after 25 min. 1 no response after 30 min
VIII	Rotation dish	14 C	18 C	1.30	1 46	12	15	12 hrs 25 min	5 responded till end of experiment
	Control	14 C	17 7 C	1 39	1 52	13	15	11 hrs.	2 no response 1 no response after 1 hr 1 no response after hrs 5 min 1 no response after 3 hrs., 35 min
VII	Rotation dish	16.8 C	18 C	1 36	1 62	13 9	16 8	7 hrs 25 min	5 responded till end of experiment
	Control	16 8 C	17 8 C	1 45	1 53	14.8	16	5 hrs 30 min	1 no response 2 no response after 40 min 2 no response after 1 hr 15 min
IX	Rotation dish	15 8 C	18 5 C	1 65	3 14	16	33	4 hrs. 45 min	5 responded after 3½ hrs before glass cover shifted
	Control	15 6 C	18 4 C	1 65	1 69	16	17	5 hrs 35 min.	1 no response 3 no response after 55 min 1 no response after 1 hr 10 min.

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* The glass cover slid to one side thus exposing a small part of the water to air for the last hour

the slow rate of oxygen diffusion is considered, it is evident that the sedentary larvae will suffer from lack of oxygen when the amount in the immediate surroundings is either exhausted or reduced to a critical point This supposition also explains how the moving water eliminates this deficiency by providing for a constantly changing supply of the water over the anal gills and body surface The uniformity of results from this series of experiments gives strong evidence for this function of the current, at least for water with low oxygen content

The records also show that, with the increased dissolved oxygen, the larvae continued active longer both in the rotation dish and the control In Experiment VIII, one larva responded after having been in the standing water (oxygen content of about 15 per cent saturation) for 3½ hours This corresponds closely with results obtained from the standing water series in bottles In the rotation dishes, when the dissolved oxygen content was 12–14 per cent of saturation, the larvae were still active after 7–12½ hours' exposure This record shows definitely that the oxygen requirement of the larvae is not as high as generally claimed

GENERAL DISCUSSION

Evidence is obtained from this study on the various factors of a normal running-water habitat that Simulium larvae have a *definite requirement for current*, and that the high dissolved oxygen content of the water is *not* the determining factor for their presence or absence, as has heretofore been so frequently stated This is also contrary to the conclusions of Hubault (1927), as described by Zeinat in *Biological Abstracts*, 2 (1928) 832, for the animals living in swiftly running streams The surface water in the comparatively slower and quieter portions of a stream was found to have practically the same dissolved oxygen content as that of the swifter and more agitated parts, and it is likewise shown by experiments that the larvae survived an exposure of 12½ hours to a low oxygen content of 13 per cent saturation Therefore, the occurrence of larvae in only the swiftest parts of a stream cannot be explained by the supposition that their oxygen requirement is so high that the slowly moving water cannot satisfy it When the natural habitats are examined, as for instance near the source of Maple River, there is a definite minimum rate beyond which no larvae occur Eggs were frequently found on plants in the shallows, where the current was very weak or wholly absent, and no larvae became established after hatching On the other hand, along the margin of the lake near the beginning of the river, where the quiet lake water begins to become converted into running water, scattered colonies of larvae were well established in current rates never lower than 0 58 foot per second, a great majority of the rates were higher Furthermore, the observations on the behavior of larvae after transplantation to currents near the neighborhood of the minimum rate show how they respond to the decrease in the current and desert the new locality for no other cause It seems, therefore, safe to conclude that the larvae have an *inherent requirement for current* Furthermore, there is some evidence that the accumulation of sediments may also be influential, to some extent, in determining the suitability of a certain current

After material is brought in from the field and left in standing water, large numbers die within a short time, as was observed by previous investigators, but the surviving ones live many more days in the same water after the removal of the dead bodies If the oxygen content in the water failed to meet the requirement of those that died, it should not be able to sustain the remainder This seems to indicate that the first large mortality was not because the dissolved oxygen present per unit volume was too low, but probably due to some result of overcrowding of larvae in a comparatively small container

The food factor has also been studied, it proved to be of secondary importance as compared with the current Larvae have been observed to endure practically complete starvation for 7–9 days, but those of medium and large sizes continued to develop in the experimental trough with filtered lake water, the food supply of which was almost, if not completely, removed The only effects were that the pupation period was somewhat prolonged and the pupating larvae, as shown by cocoon size, were proportionately smaller than those in the control trough

SUMMARY

1 New contributions not easily summarized have been made to the general biology of the different stages of Simulium and are presented in Part I of this paper

2 For the first time an observational and experimental study was made of the running-water habitat of Simulium

3 The current rates in the natural habitats were measured and found to be from 0 56 to 2 75 feet per second, or even higher where larvae were attached in more or less vertical falls

4 By means of transplantation and current experiments in the natural habitat, the following results were obtained

(*a*) The minimum current rate for larvae may be different in different streams The difference in the minimum rates in Maple River and Carp Creek was found to involve a difference in the food supply of the water, in Maple River, with a rich plankton, the minimum rate was 0 58 foot per second, but in Carp Creek, with its great paucity of plankton organisms, the minimum rate was 1 13 feet per second

(*b*) The minimum current rate for the larvae in the same stream may be different at different points within short distances, largely determined, apparently, by the rate of sediment accumulation

(*c*) The minimum current rate for the establishment on larvae after transplantation may be different, depending on the abrupt or gradual reduction of current, the rate being lower in the latter case

(*d*) Upon transplantation to a current much weaker than that in the original habitat, some of the larvae voluntarily deserted the new locality within a few minutes The number thus disappearing became larger as current rate approached the minimum or fell below it Since all the physical and chemical conditions, except that of current, were identical, this behavior seems to be a response to the current rate as such and indicates an *inherent requirement for current* This conclusion is further supported by the observation that in other experiments on reduced food supply or low dissolved oxygen content, but with normal current, the larva did not desert the point of attachment (*e*) The highest current rate obtained in trough experiments, 6 feet per second, proved to be below the possible maximum

5 The food factor was studied by the use of filtered lake water in current troughs Larvae of medium and large sizes continued to develop and transform to adults in this water with its much reduced food supply, the only effects being a somewhat prolonged pupation period and a slightly reduced size of the pupating larvae A small number of larvae have been found to stand practically complete starvation for 7–9 days

6 The problem of oxygen supply has been studied in both standing and running water The following results were obtained

(*a*) Larvae have been kept in standing water in open vessels for 14 23 days, with the majority living 6–9 days This contradicts the claim that standing water can never meet the supposed high oxygen demand of the larvae

(*b*) Analysis of the dissolved oxygen in water from both the quiet and the agitated portions of the different Simulium streams has shown that this oxygen content is practically the same This fails to support the general supposition that the larvae occur in the agitated water because of its distinctly higher oxygen content

(*c*) Experiments involving the use of water with much reduced quantities of dissolved oxygen showed that in such waters the presence of current enabled the larvae to live for prolonged periods, while in the absence of current the larvae succumbed within short periods The same result occurred even when the standing water had a much higher dissolved oxygen content

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